

NEST-SITE LIMITATION, NEST PRECISION, AND
NEST SITE SELECTION IN A CAVITY-NESTING BIRD COMMUNITY

By

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TABLE OF CONTENTS

	Page
ACKNOWLEDGMENTS	iii
ABSTRACT	iv
CHAPTERS	
1 INTRODUCTION	1
Background	1
Study Site	3
Study Species	3
Study Questions	3
2 DO NESTS AFTER LIMIT REPAIRING DOMESTERS OF SECONDARY CAVITY NESTING BIRDS?	4
Introduction	4
Methods	7
Results	15
Discussion	25
Conclusions	30
3 NESTING SUCCESS OF THE GREAT-ORIENTED FLYCATCHER IN NEST BOXES AND IN TREE CAVITIES ARE NEST BOXES SAFER FROM NEST PREDATION?	34
Introduction	35
Methods	38
Results	39
Discussion	44
Summary and Conclusions	50

4	LIFE HISTORY TRAITS IN CAVITY-NESTING BIRDS: WHY IS NESTING SUCCESS GREATER IN EXCAVATIONS THAN IN NON-EXCAVATIONS?	11
	Introduction	11
	Methods	14
	Results	18
	Discussion	21
	Conclusions	24
5	CONCLUSIONS AND SYNTHESIS	31
	Synthesis	31
	Research Needs	32
	LITERATURE CITED	35
APPENDIX A	RELATIVE ABUNDANCE OF BIRDS IN SLASH PINE PLANTATIONS - CAMP BLANCKING TRAPLINE SITE, FLORIDA, 1973-1978	58
APPENDIX B	MAXIMUM DAILY SURVIVAL RATES OF CAVITY-NESTING BIRDS AT EACH STAGE OF THE NESTING CYCLE	100
APPENDIX C	LITERATURE REVIEW OF DATA ON NESTING SUCCESSION OF CAVITY-NESTING BIRD SPECIES THAT OCCUR IN THE STUDY AREA	104
	GEOGRAPHICAL SKETCH	106

Abstract of Dissertation Presented to the Graduate School
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NEST-SITE LIMITATION, NEST FIDELITY, AND
NEST-SITE SELECTION IN A COWBIRD-NESTING-BIRD COMMUNITY

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I studied the abundance, nest-site selection, and nesting success of cavity-nesting birds in a pine forest dominated by 11-40 year-old slash pine (*Pinus elliotti*) plantations in northern Florida during 1995-1998. My research focused on two primary questions: (1) Are cavity-nesting bird populations limited by nest-site availability? (2) Is cavity-nest occupation with risk of nest predation?

In a controlled, replicated nest-box experiment, breeding densities of nest occupancies increased on 8 treated plots but remained unchanged or decreased on 4 control plots without nest boxes. Species such as the Great-Crowned Tityra (*Myiarchus cinerascens*) that displayed no evidence of nest-site limitation by usage were nest-site limited whereas species such as the Carolina Wren (*Troglodytes aedon*) that were opportunistic in their choice of nest sites (i.e., using natural cavities and crevices) were not nest-site limited. The large number of unoccupied nest boxes (from three years after their

conclusion) suggests that habitat quality may set an upper limit on the numbers of breeding birds in these young forests.

I measured 228 nests of 11 species (6 excavators, 5 non-excavators) in late spring. May field estimates of nest success were highest for the Downy Woodpecker (*Picus pubescens*) (70%) and Red-bellied Woodpecker (*Melanerpes carolinus*) (60%), and lowest for the Eastern Woodrat (*Nutallia viellii*) (0.3%). Nest predation by red snakes (*Elaphe app.*), southern flying squirrels (*Glaucomys volitans*), and other species was the most common source of nest failure. Nest predation rates in this study were much greater than those documented in other studies for similar cavity-nesting species. Contrary to previous life history studies, I found no significant differences in clutch size or daily nest survival rates between excavator and non-excavators. These life history relationships need further exploration across a range of sites.

I found a variety of evidence supporting the hypothesis that nest predation is positively correlated with cavity age. Nest success was greater in newly excavated cavities than in cavities that had been used the previous year. Egg disappearance in nest boxes increased during the second year of their availability, probably as a result of nest predation learning the locations of profitable prey items.

CHAPTER 1 INTRODUCTION

Background

Since the late 1950s, conversion of natural longleaf pine (*P. taeda palustris*) forests to even-aged plantations of slash pine (*P. elliotii*) and loblolly pine (*P. taeda*) has substantially reduced the range of longleaf forest throughout the southeastern United States. The longleaf pine ecosystem now occurs in less than 1 % of its original pre-Columbian range (Parks 1985, Ford 1985). In Florida, even-aged pine plantations managed for pulpwood have replaced most of the longleaf forest.

The biodiversity of pine forest communities in the southeastern coastal plain has been eroded by these forest management practices (Rippling and Lohrby 1987). Ground-nesting species have been especially affected. Fifty years ago, the woodpecker fauna in northern Florida was diverse, with the Red-headed Woodpecker (*Melanerpes formicivorus*) and Red-bellied Woodpecker (*Parus bicolor*) common across a range of plant communities (Davis 1911). Today, a single resident species, the Red-bellied Woodpecker (*Melanerpes formicivorus*), is predominant throughout northern Florida (Parks and Parks 1981, also see Appendix A).

Banding Bird Survey (BBS) data indicate that many ground-nesting species in Florida have experienced population declines in recent decades. Cox (1987) analyzed BBS data from 1967-1983 and demonstrated that while 1 of 20 (5%) ground-nesting

species were declining, only 3 of 45 (14%) non-cavity-nesting species were declining ($\chi^2 = 1.75$, $df = 1$, $P = 0.187$). During the 1980s, population declines of the Eastern Bluebird (*Sialia sialis*) were more severe in Florida than in any other southern state (Jensen and Deane 1994).

Population declines of cavity-nesting birds have been attributed to habitat degradation caused by intensive forest management practices (Cox 1991, Jackson 1999, Engstrom 1993), but little research has been done on the specific mechanisms that limit these species. Because pine plantations are typically young stands managed on short rotations, most standing dead trees (snags) may be too small in diameter to provide suitable for many cavity-nesting birds. Moreover, McCune et al. (1994) argued that short-rotation plantations had the lowest densities of snags of any forest type in Florida.

Currently, active research and management in southern-pine forests focuses primarily on the endangered Red-cockaded Woodpecker and the common longleaf pine snags where it nests. At the same time, however, forestry practices that occur outside these isolated longleaf forests continue to have a tremendous impact on other cavity nesters. In their landmark monograph on cavity-nesting birds, Raphael and White (1984) concluded that the determination of reproductive success or failure to nest-site characteristics and other habitat features should be a wildlife management priority. However, almost two decades later, this type of information is still lacking in Florida. Despite the diversity of planted pine, mature cypress, oak, and oak-pine riparian areas, southern pine plantations are unknown for almost all species of cavity-nesting birds.

Most of our knowledge about cavity-nesting birds is based on more than a half-century of Old World species. Ecologists have only recently begun to conduct intensive field study of cavity-nesting birds in natural nest sites on wildlife refuges and about various life history theory and community ecology (e.g., Li and Martin 1999, Martin and Li 1992, Powell et al. 1997). With this in mind, I conducted a comprehensive 4-year study of the ecology of cavity-nesting birds in managed pineyards in northern Florida.

Study Site

Camp Bowling, Training Site (CBTS) is a Florida Department of Military Affairs Army National Guard facility encompassing 16,000 ha in Clay County, Florida. Pineyards at CBTS are currently in poor condition because of the conversion of most of the longleaf pine (*Pinus palustris*) and scruboaks to slash pine plantations and many years of fire suppression (Peters and Jackson 1994). In these respects, I believe they are more typical of pineyards in contemporary Florida.

Study Species

As many as 15 species of cavity-nesting birds occur in the pineyards of northern Florida (scientific names in Table 1-1), although one is a wintering species (Yellow-bellied Sapsucker), one is increasingly rare (Blue Owl), and most are regularly a "nest" and "empty" species and not an obligate cavity species (Carolina Wren). That leaves 11 cavity-nesting species that are potential breeders in managed pine forests on the CBTS study area. Several of these species were rare in CBTS plantations (see Appendix A).

Table 1.1. Cavity nesting bird species occurring in pinehills at Camp Blanding Training Site

Common name	Scientific name	Least ¹	High nest ²	Least ³
Wood Duck	<i>Aix sponsa</i>			
Scrubwren: American Redtail	<i>Falco sparverius palmeri</i>	X	X	X
Blue Owl	<i>Nyctalex</i>		X	
Eastern Screech-Owl	<i>Otus asio</i>			
Parula Woodpecker	<i>Dryocopus pileatus</i>		X	
Northern Flicker	<i>Colaptes auratus</i>		X	X
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>			
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>		X	X
Red-necked Woodpecker	<i>Picoides borealis</i>	X	X	X
Gray Woodpecker	<i>Picoides villosus</i>			?
Downy Woodpecker	<i>Picoides pubescens</i>			
Yellow-bellied Sapsucker ⁴	<i>Sphyrapicus varius</i>			
Great Crested Flycatcher	<i>Myiarchus cinerascens</i>			?
Tufted Titmouse	<i>Parus tyto</i>			
Cerulean Chickadee	<i>Parus ceruleus</i>			X
House Wren	<i>Troglodytes aedon</i>			X
Carolina Wren	<i>Troglodytes carolinensis</i>			
Eastern Bluebird	<i>Sialia sialis</i>			X

¹ Endangered or threatened species

² Species given high (X/HT) biological score or action score by the Florida Fish and Wildlife Conservation Commission (McIlroy et al. 1998)

³ Breeding Bird Survey data indicate statewide habitat related population decline (Cox 1981, Royside et al. 1994)

⁴ Widespread, does not breed in Florida

Research Questions

One of the central questions of interest to both ecologists and wildlife managers is whether cavity nesting bird populations are limited by the availability of nest cavities. Although a generally accepted concept, nest site limitation rarely has been studied effectively with manipulative experiments. Thus, I conducted a controlled, replicated experiment to test for nest-site limitation in Florida gull populations. I discuss my findings in Chapter 1, with special focus on interspecific variation in nest-site limitation.

Nest boxes are commonly used in study areas life histories and population dynamics, but in recent years there has been considerable concern for a variety of reasons (e.g., Miller 1985) including the concern that nest boxes might be safer than predators than natural sites. In Chapter 2, I test this hypothesis by comparing reproductive success of Great Crested Flycatchers (*Myiarchus cinerascens*) in nest boxes with those in hole cavities.

Although nest predation has become an important focus of research in avian ecology during the last decade, relatively little attention has been directed towards cavity nesting birds, in part, because of the difficulty in assessing and comparing the contents of cavities at suitable stages. In Chapter 3, I examine nesting success and nest predation rates for a community of cavity-nesting birds, focusing on the differences between excavator species and non-excavator species. I evaluate several hypotheses for why non-excavators are more vulnerable to nest predation than excavators.

Finally, Chapter 4 integrates the conclusions of each chapter and identifies key areas for future research.

CHAPTER 2

DO NEST SITE LIMIT BEEHIVING DENSITY OF SECONDARY CAVITY NESTING BIRDS?

Introduction

Nest sites are often considered to be the primary factor limiting the densities of secondary (i.e., non-maturing) cavity nesting birds (CNAbs) (e.g., van Heerwaarden 1977, 1981, Tammes et al. 1978, Cody 1982). However, despite decades of research on cavity-nesting birds, none of the nest-site limitation hypotheses by manipulative experiments, which include knowledge of actual densities, adequate controls, and replication (Harrison 1983), are still intact. In a recent review, Newton (1986) concluded that most evidence for nest-site limitation in cavity nesting birds is circumstantial. Among studies that added or subtracted nest sites to the cavity-nesting birds, Newton (1984) identified only 8 studies that included both controls and pre- and post-manipulation data; of these 8, only 3 (Tammes and Økland 1972, Brown and Balda 1980) had replicate study plots. Other common flaws in previous tests of the nest-site limitation hypothesis include lack of spatial independence of experimental and control plots (e.g., East and Pomeroy 1982, Baumgardner and Balda 1982) and inadequate controls because of placement of study plots in desirable plant communities (e.g., Breck 1982). Inadequate experimental controls can mask apparent experimental effects open to alternative explanations such as temporal and spatial variation in habitat quality. In summary, there have been few

controlled nest-box experiments where the study design allowed unambiguous interpretation of the results.

Most nest-site limitation studies have been conducted on a small number of species inhabiting European forests, especially the Great Tit (*Parus major*) and Pied Flycatcher (*Uchalcia hypoleuca*). Controlled nest-box experiments have not been associated with cavity-nesting birds in pine forests of the southeastern United States. Red-bellied juncos at southern pine forests are commonly considered to limit the availability of deadwood (snags) that provide nest sites for cavity nesters (McCune et al. 1986, Jackson 1993), yet the nest-site limitation hypothesis has not been tested experimentally. The primary objective of this study was to test the hypothesis that nest-site availability limits the breeding densities of SCNs in pine forests in southern Florida.

Methods

Study Plots and Experimental Design

Fieldwork was conducted on 12 study plots in slash pine (*Pinus elliottii*) plantations at Camp Blanton Training Site, a Florida Army National Guard facility in northern Florida (Fig. 1-4). Plantations were 31-48 yr-old even-aged stands that had grown unharmed for more than three years. To control for variation in site productivity, I distributed study plots evenly between main "thicketed" sites and more "opened" sites. "Thicketed" plantations were densely stocked and characterized by moderately to poorly developed canopies and a dense shrub layer of gallberry (*Myrsine glabra*), saw palmetto (*Serenoa repens*), and various woody vines (Mendenhall and Plummer 1992). "Opened" plantations were moderately stocked and characterized by well-developed canopies



Figure 2-11. Location of twelve 10-hectare photomonitoring plots at Camp Blanding Training Site, Clay County, Florida, 1993-1994

each and a patchy understory of hickory oak (*Quercus laevis*) saplings. Before the experimental plantations, the smallhill sites were dominated by longleaf (*Pinus palustris*) smallhills (open pine woods) with a ground cover of perennial grasses and forbs (Stynes 1998). Within each study plot, I removed low vegetation at point count stations (Stynes et al. 1997) and marked snags > 10 cm diameter at breast height (d.b.h.) on two 5-m x 5-m transects to develop visual profiles for each plot (Table 2-1). Most snags were too small for excavation by woodpeckers; <2% of plantations snags were >22 cm d.b.h. (capped trees).

Study plots were of equal size (30 ha) and dimensions (250 m x 400 m) and situated as far as possible (typically >75 m) from roads and other openings. Study plots were broadly dispersed to minimize spatial autocorrelation: the northeastern study plot was 1.1 km distant from the northeastern plot, and the northeastern study plot was 4.2 km distant from the southwestern plot (Fig. 2-1). Nearest-neighbor distances between study plots ranged 1.2 km (range 0.5–2.8 km). A strip of wetland forest separated the two study plots that were only 0.5 km apart.

After two years of breeding bird surveys to document initial conditions (1994–1996), I applied treatments randomly in a balanced design (Table 2-2). Prescribed burns were conducted on 1 burned plot and 2 smallhill plots during January–February 1997. Waterfowl (northern bobwhite and mallard) frequency (i.e., foraging <10% reduction in the height of shrubs and saplings that did not cause tree mortality). During the first week of March 1997 (> 1 month before the breeding season for all S-O species) I censused nest boxes on all of the burned plots and on 4 of the unburned plots. Spring 4 indicated

Table 1.1 Stand profiles of slash pine plantations in two forest types: Canopy Shading
Training Site, Florida, summer 1991

Forest type	n	Canopy height	Total basal area	Open basal area	Basal/ha ^a
		(m)	(m ² /ha)	(m ² /ha)	
Fullsun	4	29.4 (8.5) ^b	30.4 (2.2)	9.2 (0.3)	21.1 (2.8)
Shade	4	17.3 (3.1)	24.3 (2.5)	5.1 (0.2)	24.8 (2.1)

^a Basal area basal area, \pm SE can diameter at breast height.

^b Mean (SE).

Table 1.2: Experimental design used for part of our (anonymous) Treatments (O = no manipulation, K = new bones added, Y = new bones added after control hand was randomly applied/within 15 min type

Plot #	2015	2016	2017	2018
Plots 1-6				
1	O	O	O	O
2	O	O	O	O
3	O	O	X	X
4	O	O	X	X
5	O	O	Y	Y
6	O	O	Y	Y
Plots 7-12				
7	O	O	O	O
8	O	O	O	O
9	O	O	X	X
10	O	O	X	X
11	O	O	Y	Y
12	O	O	Y	Y

plots without nest boxes or rodents (Table 2.2). Two years of breeding bird surveys were conducted to assess the effects of treatments (1993-4, 1996).

Nest Boxes

I constructed 108 nest boxes three-meters tall under oaks. I used a range of dimensions to accommodate all species of BOM, except double-crested cormorants that breed in Florida grasslands. Nest boxes differed in width (two dimensions) 30.2 x 19 cm or 14.8 x 11.2 cm, in the diameter of the entrance hole (2.5 cm or 3.1 cm), and in floor height above ground (1.7 m or 4.3 m). On each nest box plot, I installed all nest boxes (4 per ha) at 50-m intervals in a standardized array. The nest box array was a balanced, 3 factor design: box size (small vs. large) x hole size (narrow vs. wide) x box height (low vs. high). I placed all nest boxes with the entrance hole oriented to east by southeast, because easterly or southeasterly orientations are preferred by many cavity-nesting bird species (Coxsey 1973, Pukowski 1979, Mollitt 1979, Randall and Robertson 1994).

I inspected the contents of each nest box once every 10-14-d during April-May and once every 14-21 d during June-July. As soon as I observed nesting activity in a nest box, I monitored the nest box regularly at 3-d intervals. High nest boxes were reached with an aluminum extension ladder. For analysis of nest box use, a nesting attempt was defined as a nest where ≥ 1 egg was laid. Southern flying squirrels (*Glaucomys volans*) and other non-avian mammals were not discouraged from using nest boxes, because I wanted to study context-moderating factors for birds under natural conditions. Squared roost sites were defined as those nest boxes in which flying squirrels were observed on ≥ 2 occasions within a season.

Nest Searches and Nest Monitoring

I used standard methods (Martin and Geupel 1993) to search for SCM nests at two research study plots from early April through early July, 1994-1998. I maintained search plots among plots and visit periods (early morning, late morning/late afternoon) comparable search effort among study plots. Once nests were located, nests were probed regularly at 3-4 d intervals to assess nesting status (Martin and Geupel 1993, Ralph et al. 1993). (See Chapter 3-4 for details on techniques used for monitoring cavity nests.)

Estimation of Nest Success

I used the extensive point count method (Ralph et al. 1993, Wilson et al. 1995) to estimate densities of breeding birds at study plots. Extensive point counts differ from extensive point counts in that points are established uniformly close together within a nest search plot or nest site plot, and count data within each plot are pooled for analysis (Ralph et al. 1993).

Point-count survey methods followed standards outlined by Ralph et al. (1993) remain were conducted within 3 hrs post sunrise, no counts were made during rain. Fly or strong winds, birds not flying above the canopy were recorded separately (not counted within a fixed width circle) were not recorded if they were observed moving in an adjacent fixed-width circle. I conducted all point-count surveys in duplicate with observer bias. I substituted 3-minute count period because 84% of the species in that system were detected within the first two minutes (unpubl. data), and a longer count period would increase the likelihood of double counting (Karr and Ramsey 1981). Data

Two pilot studies in August 1994 and April 1995 demonstrated the effective detection distance was >12 m for most species, including all cavity-nesting species. Accordingly, I established six 15-m radius point-count stations spaced 120 m apart within each plot. I recorded birds within the 12-m fixed-radius separately from birds >12 m from the observer (Stuart et al. 1984, Bailey et al. 1992). Each point-count station was sampled three times per year, at intervals of 20 weeks between 20 April and the second week of June.

Analysis of Experimental Effects

I pooled fixed-radius point-count data during each visit to a study plot because each plot was considered an experimental unit for analysis (Ralph et al. 1992). Within each plot, I used the maximum pooled count for each species for comparison among plots, treatments, and years. Count data were not transformed for analysis because of homogeneity of variances across treatments and years. I analyzed experimental effects with a mixed model analysis of variance (ANOVA) utilizing generalized least squares estimation (PROC MIXED), SAS Institute 1997). The model included four factors: Treatment (Control vs. nest box vs. treated with nest box), Forest (Oakwood vs. scruboak), Time, and the random plot effect. I modeled the differences in count data between pre-treatment years (1995, 1996) and post-treatment years (1997, 1998) by using an average of the two pre-treatment years as a covariate (covariate analysis indicated that pre-treatment years did not differ). Post-treatment years were tested separately in the ANOVA because I wanted to determine if responses to treatments changed over time. Goodness of fit criterion (Satterthwaite's Bayesian Criterion) indicated that a model including interaction terms (Treatment \times Forest, Treatment \times Time) best described the data for each

species. For significant factors in the model, pairwise differences of least-squares means (PROC MIXED) determined the relationships between variables.

Results

Post-Crest Surveys

Effects of nest box treatments on cavity nesting bird populations

Secondary cavity nesters – I detected 4 species of secondary SCNs during three select post-crest surveys. Great Crested Flycatcher (*Myiarchus cinerascens*), Tufted Titmouse (*Parus cyaneus*), Carolina Wren (*Troglodytes halimicus*), and Eastern Starling (*Sterea vulgaris*).

For all SCN species combined, the mixed model ANOVA indicated that Treatment was the only significant factor ($F = 7.17$, $df = 2,3$, $P = 0.01$) explaining the change in counts between pre-treatment years (1993, 1994) and post-treatment years (1997–1998). After treatments were applied, SCNs increased on treated plots but decreased slightly on control plots (Fig. 2-2). In the two years post-treatment, differences of least squares means indicated that means (mean \pm SE) were significantly greater ($P = 0.01$) in subnests/plots with nest boxes (NB) (2.3 ± 0.7) than in control plots (1.6 ± 0.4). Counts also were significantly greater ($P = 0.02$) in treated plots with nest boxes (BMB) (2.6 ± 0.4) than in control plots. SCNs did not differ between NB plots and BMB plots.

The Treatment \times Year interaction term approached statistical significance in the mixed model ($F = 2.18$, $df = 2,3$, $P = 0.11$), reflecting the different rates at which SCNs responded to nest boxes on NB and BMB plots. On NB plots, SCNs increased at pre-

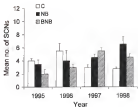


Figure 2.3: Mean counts of secondary cardiomyocytes (SCNs) on placental study plots before (1995-1996) and after (1997-1998) treatment (C = control, NB = enhanced plots with no treatment, BNB = enhanced plots with treatment). Bars represent standard error.

treatment levels in 1997 and increased sharply in 1998, while on ENB plots SCNs declined or remained constant in 1997 and declined slightly during 1998 (Fig. 3D). The largest increase in SCNs from one year to the next occurred in the first post-treatment year in ENB plots, when SCNs increased nearly twofold (Fig. 3-2).

Primary cavity nesters. I selected 8 species of primary (i.e., noncavity) cavity nesters, including the Carolina Chickadee (*Parus carolinensis*), Brown-headed Nuthatch (*Sitta pygmaea*), Red-bellied Woodpecker (*Colaptes cafer*), Red-headed Woodpecker (*M. erythrocephalus*), Downy Woodpecker (*Picus pubescens*), Red-streaked Woodpecker (*P. borealis*), Northern Flicker (*Colaptes auratus*), and Pileated Woodpecker (*Dryocopus pileatus*). Although 8 species of woodpecker were recorded, Red-bellied and Downy Woodpeckers accounted for 70% of all woodpeckers counted within 100 meters post-treatment. Counts of primary cavity nesters did not vary among treatments, either for all species combined ($P = 0.23$) or for any individual species ($P > 0.05$).

Inter-specific variation in BCF response to aerial herbivory

Five Great Crested Flycatchers. Treatment was the only significant factor in the mixed model ANOVAs ($P = 0.01$, $d.f. = 1,5$, $P = 0.005$). After treatments were applied, Great Crested Flycatchers increased on treated plots but decreased slightly on control plots (Fig. 3-3). In the two years post-treatment, counts in ENB plots (2.9 ± 0.4) were significantly greater ($P = 0.002$) than counts in control plots (2.3 ± 0.3), and counts in MB plots (2.4 ± 0.4) were significantly greater ($P = 0.002$) than counts in control plots. MB plots and ENB plots did not differ. Great Crested Flycatcher nesters reached their peak

during the study or the BSB plots during the first year after beaver were introduced (Fig. 2-1).

The Tuffed Titmouse exhibited a response to nest beaver similar to that of the Great Crested Flycatcher: counts increased threefold on island plots after treatments were applied (Fig. 2-4). Before nest beaver were introduced, Tuffed Titmouse were not recorded in band-radius point counts on any BSB plots in 1995 and on only one BSB plot in 1996. However, Treatment was not significant in the mixed model ANOVA ($F = 0.10$, $df = 2,8$, $P = 0.90$), in doubt, largely because of the small samples involved. Tuffed Titmouse densities (Fig. 2-4) were matched those of the Great Crested Flycatcher (Fig. 2-3).

Carolina Wrens showed no response to treatments (Fig. 2-5). The Carolina Wren was the only SCM species that did not exhibit an immediate response to nest beaver on BSB plots in 1997. Eaten was the only significant factor ($F = 9.62$, $df = 1,8$, $P = 0.01$), explaining the change in counts between pre- and post-treatment years. The only were Carolina Wrens more common in Plateau plots than in Sandhill plots, but the difference in relative abundance between Forest type grew larger over time, regardless of treatment.

Eastern Bluebirds were seldom recorded on plateau study plots. No factors were significant in the mixed model ANOVA, although the small samples provided made it difficult to detect differences. However, the fact that bluebirds were not recorded in band-radius point counts on any plots until after nest beaver were introduced (Fig. 2-6) strongly suggests that they responded to the nest beaver.

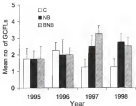


Figure 2.3: Mean counts of Giant Crested Flycatcher (GCFLs) on plantation study plots before (1995-1996) and after (1997-1998) treatment. C = control, NB = reduced plots with nest boxes, C+NB = treated plots with nest boxes. Error bars are standard error.

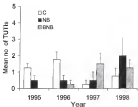


Figure 2-4 Mean means of Tuffet Vectors (TUTVs) on phytoseiid study plots before (1995-1996) and after (1997-1998) treatments (C = control, NB = undisturbed plots with new boxes, BNB = treated plots with new boxes). Bars equal one standard error.

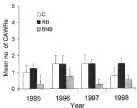


Figure 2.3 Mean counts of Caneless Wrens (CAWRs) on plantation study plots before (1995-1996) and after (1997-1998) treatments (CC = control; HB = submersed plots with wet forest; BNB = burned plots with wet forest). Bars equal one standard error

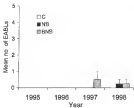


Figure 2.4. Mean counts of Eastern Bluebirds (EABs) on phytosan study pine before (1995-1996) and after (1997-1998) treatments (C = control, NB = enhanced plots with nest boxes, BMB = treated plots with nest boxes). Bars equal one standard error.

Nest Monitoring

Patterns of nest box occupancy

I recorded 37 nesting attempts in nest boxes during 1997–1998, including 18 (49%) Green-Crowned Flycatcher nests, 11 (30%) Tailed Tropicbird nests, 4 (11%) Eastern Bluebird nests, 3 (8%) Carolina Wren nests, and 1 (3%) Eastern Gnatcatcher (Gnatcatcher nests). Gnatcatcher nests were only in nest boxes that had three entrance holes enlarged by sparrows. No woodpecker species nested in nest boxes, but Red-bellied Woodpeckers were observed using 19 nest boxes on eight nest sites. Boxes used as woodpecker nest sites contained seeds and other food debris and others were located >50m from an active Red-bellied Woodpecker nest as a place trap. Overall mean occupancy of nest boxes, including woodpecker nest sites, increased from the first year to the second year (8% and 14% in 1997 and 1998, respectively). BCS nests were built in 7% and 11% of the nest boxes in 1997 and 1998, respectively. Flying squirrel used nest boxes on all study plots, 36 (22%) and 36 (19%) nest boxes were used as roost sites by flying squirrels in 1997 and 1998, respectively.

Nests as free-ovulation versus nest boxes

The total number of BCS nests on study plots increased after nest boxes were introduced (Table 2-1). The total number of BCS nests (including Carolina Wren nests) increased twofold in 1997 (27 total nests) and increased six-fold by 1998 (48 total nests) because of the large numbers of nesting attempts in nest boxes (Table 2-2). The relative abundance of BCS species was proportionately similar in cavity nests versus nest boxes. BCS cavity-nests monitored during 1996–1998 included 18 Green-Crowned

Table 2.3: Means of secondary cavity-nesting birds (Great Crested Newgutter, Titled Terns, Eastern Blackbird, Eastern Scopsch Owl)-based larvae numbers and in nest losses, both before (1998) and after (1999-2008) treatments applied. Carolina Wren nests are not included because they nested only in nest boxes.

	Pre-treatment		Post-treatment years			
	LRR		LRR		LRR	
	Cavity	Nest	Cavity	Nest	Cavity	Nest
Control plots ($n = 4$)	4	— ^a	3	—	3	—
Most loss plots ($n = 4$)	5	—	3	4	3	13
Fragment nest loss plots ($n = 4$)	4	—	1	14	3	19
Total	13	—	7	24	9	32

^a Nest losses not available

Tyrannulet nests, 4 Tufted Titmouse nests, 1 Eastern Bluebird nest, and 1 Eastern Heron's Owl nest.

Nest birds also indicated that nesting activity on NB plots lagged behind that on EB-0 plots. SCN birds made little use of nest boxes on NB plots until 1998, the second year after the boxes were put in place (Table 3-15).

Discussion

Response Of Cavity-Nesting Bird Populations To Plant Box Treatments

Nest-site availability was a limiting factor on the breeding success of SCN birds. Numbers of SCN birds recorded during the breeding season increased significantly on treated plots after nest boxes were introduced. The number of SCN nesting attempts observed on treated plots also increased several fold. Together, these data indicate that cavities were in short supply before nest boxes were introduced. Populations of cavity-nesting species did not increase because they did not use nest boxes for nesting during the course of the study.

Increases in SCN numbers are even more striking in light of the modest decreases that manifested themselves on control plots (Fig. 3-2). Because control plots were not different from treated plots in tree density, tree age, or vegetation composition, the randomized, replicated-experimental design suggests that SCNs would have declined on other plots if not treated with boxes. It is very unlikely that SCN birds moved from control plots to treated plots, because interplot distances were several times larger than the territory sizes of these species (Emmons and Pomeroy 1984, Lanyon 1997, Gorman

and Plummer 1989]. Even if some individuals did move between plots, the slight decline in number of nesting nests on control plots (from 4 to 3 in each of the following years, Table 3-5) cannot account for the large increase in the number of nest nests on treated plots during 1993-1994.

Interspecific Variation in SCN Nest-site Limitation

Populations respond to nest losses by individual species ranged from moderately high (Great Crested Flycatcher) to low (Eastern Bluebird) in response to all (Carolina Wren). Two factors probably account for interspecific differences observed in this study: different levels of reliance on cavities expressed in stage and differences in local population densities.

Great Crested Flycatcher

Great Crested Flycatcher responded more strongly to the addition of nest boxes in young plantations than did Tufted Titmouse and Eastern Bluebirds, suggesting that they probably were more nest-site limited than the other two species. Similarly, Beahm (1982) found that the neotropical Ash-throated Flycatcher (*M. cinerascens*) increased from 0 to 1 breeding pair after 38 nest boxes were added to a 14-ha plot of regrowth forest that was devoid of cavities. Walter et al. (1998) found no evidence of nest-site limitation for Ash-throated Flycatcher in a mature oak-pine woodland with abundant cavities (only 3 per ha).

Nest-site limitation in the Great Crested Flycatcher was probably related to its dependence on woodpecker excavated cavities for nesting: only 1 of the 38 (3%) cavity nests that I installed was not natural cavity in a living tree (see also Chapter 4).

Myiarchus cinerascens (see and do, not follow branches and other large-sized species when they are available (pass. obs., Lanyon 1997), but such species did not occur in 10–40 yr-old shade-pine trees. Similarly, in ponderosa pine (*P. ponderosa*), BCN species that nested almost exclusively in previously-used cavities in snags 1–4, Violet-green Swallow, *Empidonax shufeldti*, Pygmy Woodpecker, *Geopelia pygmaea*, Western Bluebird, *Sialia mexicana* exhibited greater population responses to new holes than those species that nested primarily in natural cavities and crevices (Brown and White 1988).

Tufted Titmouse

The Tufted Titmouse increased in numbers following the introduction of nest boxes but not as dramatically as did the Great Crested Flycatcher. The propensity of Tufted Titmouse to nest in natural cavities in live trees may partially explain why they did not respond to the cavities experiment as strongly as did Great Crested Flycatchers. Nest monitoring indicated that 1 of 4 (25%) incubated eggs in shade-pine trees were in the natural cavities formed between forked pine trunks (see also Chapter 4). The Tufted Titmouse's smaller body size may have allowed it to be more opportunistic in its use of natural cavities than the Great Crested Flycatcher.

Carolina Wren

Carolina Wrens showed no response to treated and, despite dense shrubland, early used nest boxes. Nest monitoring indicated that Carolina Wrens typically built nests within oak palmate shrubs or low perches in brush piles, trees, and shrubs, making their cavities dependent on tree cavities than Tufted Titmouse.

Eastern Bluebird

Eastern Bluebirds were or were not on these study plots that it is difficult to assess whether they were nest-site limited (although they did occur in very low numbers on four of the treated plots two years after nest boxes were introduced). The Eastern Bluebird's relation as a nest-dependent-excavated species (Pakeman 1976; see also Chapter 4) should make it nest-site limited, provided that it sufficiently depends on suitable habitat. Implicit in our test of nest-site limitation is the assumption of a maximum level of local abundance of a given species in the study area. For most species, local or regional population densities are usually insufficient to provide the single or fewer individuals that would limit if more nest sites were available (Pakeman 1976). Eastern Bluebird populations have declined rapidly in Florida since the 1960s (Cox 1987; Jones and Deegan 1990) and the species was uncommon or rare throughout the study area (year site 1), perhaps because of crop years of the suppression at Camp Wooding Throwing Site. Because the Eastern Bluebird prefers dense edges and openings and other plant communities that offer the trees and sparse ground cover (Cheney and Plummer 1990), these densely wooded slash pine plantations may not agree with the niche structure (Jones and Jones 1988; Jones et al. 1988) occupied by Eastern Bluebirds.

Effect of Habitat Structure on Nest-site Limitation

The degree of nest-site limitation for all birds did not vary between forest types. Birds in barrens plantations and sandhill plantations responded similarly to treatments despite marked site differences in song availability and local nest (Table 2-1). Large structural differences between plant communities might have produced different results.

Response of Nest Type: the response to nest boxes was most rapid on burned plots. SNPs increased dramatically on the burned plots with nest boxes, whereas SNPs numbers on the unburned and less plots did not increase as rapidly until 1998, the second year after treatment (Fig. 2-1; Table 2-1). Populations of many SNP species responded linearly to open microhabitats created by burning (e.g., Beck and Lynch 1976, Polakowski 1976, Brown et al. 1984, Datto 1993, Kestel and Sileo 1993). Slower discovery rates of nest boxes in SNPs plots was probably the result of an atmospheric event when winter storms had temporarily opened up the shrub layer and underlying

Other Factors Potentially Limiting Cavity-Nesting Bird Populations

Breeding populations of cavity-nesting birds potentially can be limited by other factors, including food, territoriality, and intraspecific competition for nest sites. The relatively low levels of nest box occupancy by birds (only 6% were used for nesting) could be indicative of low habitat quality (e.g., low food availability, unsuitable habitat structure). Other studies on woodland birds have demonstrated a greater response to nest boxes. For example, in thousand candelabra pine forest in Arizona, bird use of nest boxes increased from 18% in the first year of their availability to 55% in the fourth year (Brown and Balda 1982). Nest box occupancy rates in oak pine woodlands in California increased from 25% in the first year to 65% in the sixth year (Pearce et al. 1987). In a nest box study of Barnard's Gullies (*Urocyon calendula*), Sorenson (1984) found that populations that did not increase until the third year after nest boxes were introduced, he attributed this to 2-year-old chicks, which were produced in nest boxes during the first year.

entering the breeding population, it was unable to construct the additional nest because of continual tree-cutting in several nest box plots during 1999–2000. However, I continued monitoring those plots that were unaffected by forestry operations and found that <10% of nest boxes were occupied by SCNs in the third and fourth year post-treatment. Thus, there is no evidence for continued consistent use of nest boxes over time.

I found little evidence that territoriality or interference-competition were important in this system. As present densities, territorial behavior is unlikely to have been sufficient to prevent individuals from breeding. For example, territory mapping (unpublished data) demonstrated that Green-Crowned Flycatchers sometimes were strictly territorial, which suggests that territorial behavior was not lacking. Interference competition for nest sites was not observed among SCM species at natural nests in this system, although I did observe several aggressive interactions between Red-bellied Woodpeckers and Green-Crowned Flycatchers at Red-bellied Woodpecker nest cavities (pers. obs.). The large number of nest boxes occupied by SCNs or flying squirrels (approximately two-thirds of the total each year) also suggested little potential for interference competition among species. I did not observe attack or other species' usurpation of nest boxes, with the possible exception of two instances where flying squirrel nest material was found on top of what appeared to be an incomplete bird nest. In each case, it was not determined whether the birds had abandoned their nest-building efforts prior to usurpation of the box by flying squirrels.

Conclusions

Brown and Balda (1988) concluded that a given SCM population was nest-site limited only if it was dependent on cavities excavated in dead wood by primary cavity-nesters. Results of this study confirm this pattern: species that were opportunistic in their choice of nest sites were less likely to exhibit population responses to the introduction of nest boxes. Two factors are of play in determining a particular species' reliance on cavities created by excavators: whether natural cavities (i.e., those not excavated by other birds) of a sufficient size are available, and whether its nest-site preferences are generalized enough to allow it to use the types of natural cavities and cavities available. The natural cavities available at pine trees were apparently of sufficient size for most Coast Range Flycatchers.

Nest-site limitation should not be assumed for all cavity-nesting birds in all plant communities and locales. Waters et al. (1992) found no evidence that any SCM species was limited by cavity availability in an oak-pine woodland in California that had abundant natural cavities. Brown and Balda (1989) found that three SCM species were limited by nest-site availability in two open stands of ponderosa pine, but they found no evidence of nest-site limitation in a relatively dense, managed stand that contained more oaks and more snags. Natural cavities formed from decay are much more abundant in hardwood trees than in conifers (Waters et al. 1992) and tree density and tree age are positively correlated with cavity density (see Balda et al. 1987). Thus, it follows that SCM densities are most likely to be limited by nest sites in young forests and in forests dominated by conifers.

The conclusion was that nest-site availability is the primary factor limiting the breeding densities of SCN birds in an over-simplification. For example, Newton (1979, 1981) demonstrated that breeding densities of cavity nesting species can be limited by either nest sites or by food, depending on whether or not there is a sufficient supply of a particular food and place. In my study, the large number of subsequent nest losses (over three and a-half years after they were introduced) suggests that habitat quality may not be appropriate as the measure of breeding limits in these young forests.

However, if dense shade pine plantations are only marginally suitable as breeding habitat (i.e., for Eastern Bluebirds), then populations will not increase regardless of the number of cavities that become available. The immediate response of cavity systems in new bog plots that had recently been burned is consistent with the hypothesis that nest-site limitation is mitigated by habitat structure (Brown and Davis 1987). Treatment prescribed burning over a period of years would enhance habitat quality for SCNs, but long-term population effects of burning at regular intervals were outside the scope of this study. Prescribed burning occurred to facilitate the recovery and use of nest boxes by SCNs in this study. If increasing cavity-nesting bird populations is a management goal in fire-maintained habitats, such as southern pine forests, managers may find that the addition of nest boxes to newly burned sites will result in the highest local densities of SCN birds.

CHAPTER 1
NESTING SITES OF THE GREAT CRESTED FLYCATCHER
IN HOLE BOXES AND IN TREE CAVITIES
AND NEST BOXES SAFER FROM NEST PREDATION

Introduction

Raptors may not visit nest boxes the first year or two after they are erected. But it is also well recognized that nest eventually will be recognized and discovered a nest of eggs. Thereafter, it apparently visits eggs in each box it finds.

— L. B. Lindridge and C. G. Webster (1981) from "Raptor
predation on nest-boxed," *Transactions of North American
Wildlife Natural Resources Conference* 33: 189-190

Ornithologists have used nest boxes to study avian nesting habits for more than 70 years. Much of what is known about avian life histories and population dynamics is based on data from field studies that use nest boxes. In recent years, the use of nest boxes is limited and has been under criticism (Moller 1987). Some have argued that nest boxes are "false" descriptions that mislead and even mask patterns of reproduction success observed in nest-box studies may be an artifact of nesting in boxes (Schmidt 1984, 1986; Moller 1988; Papellari et al. 1993). However, rigorous field tests of this assumption have been limited. Many studies that purport to show differences between nest boxes and tree cavities have compared reproductive parameters of separate populations in different treatments (Langberg and Abshire 1997; Kuhnlein and Abshire 1992), while ignoring spatial and temporal differences in habitat quality and the density

of nest predation. For example, *Kukkonen and Ahlborn (1992)* compared nest success of *Cyanus Truncatus* (*Cyanus borealis*) breeding in nest boxes in Finland over a 9 year period versus those breeding in natural cavities in Lithuania over a 20 year period. Two studies have compared nesting success of birds using nest boxes versus those cavities in the same locality during the same time period.

Although some studies have found higher nesting success in nest boxes than in tree cavities (*Nilsson 1975, 1984; Lait and Pärssä 1984*), other studies have reported no differences between tree cavities and nest boxes (*Robertson and Russell 1990; Goffeard 1998*) or greater nesting success in cavity nests than in nest boxes (*Julle et al. 1992*). However, when differences between nest boxes and natural sites are found, they often do not occur for all cavity-nesting species within a particular study area (*Nilsson 1984; Pärssä et al. 1997*). Within a given species, reproductive success can vary considerably over space and time between nest sites (e.g., for the European Noddy, *Sitta europaea*; *Nilsson 1975, 1984, 1986; Korpimäki 1989; Akaike et al. 1991; Lait and Pärssä 1992*), highlighting obvious generalizations about differences between nest boxes and natural nest sites.

Within a particular locality, nest boxes and tree cavities can differ in several respects that are typically not measured. Because nest height (*Nilsson 1984; Li and Martin 1991*) and microhabitat structure (*Bellin-John and Pärssä 1995; Pyle 1997*) can influence reproductive success in cavity-nesting birds, comparisons between nest boxes and tree cavities can be misleading if nest boxes are not placed in similar heights and in similar microhabitats.

My objectives in this study was to compare nesting success of the Great Crested Flycatcher (*Myiarchus cinerascens*) in nest boxes and in tree cavities in the same habitats during the same years. By studying remaining individuals, I identified spatial and temporal biases in my comparisons. I also measured microhabitat characteristics at all nests to study the similarity of nest boxes and cavity nests and to assess the influence of these nest site characteristics on nest success.

Methods

Study Site and Study Species

I conducted my study at 35–40 yr-old slash pine (*Pinus elliotii*) plantations at Camp Blending Training Site, a Florida Army National Guard Training area in northern Florida. My field excursions and I searched nests in tree cavities as twitches (8-ha pine plantation study plots, one 8-ha pine plantation study plot, and one 18-ha pine plantation that excluded small patches of turkey oak (*Quercus laevis*)). Eight of these study plots were segmented with nest boxes. All 14 study plots were mature-aged pine stands lacking a well-developed understorey (see Chapter 2 for further description of the study plots). Density of standing dead trees (snags) in these stands ranged from 1.2 to 19 per ha.

The Great Crested Flycatcher was the most common secondary cavity nester (i.e. non-excavator) species on the study area. A single-banded Neotropical migrant, it returns to the study area each year during the first week of March and begins building nests in mid-to-late April.

Nest Boxes

I constructed 140 nest boxes of rough-cut cedar wood with an entrance hole (3.1 cm diameter) designed to accommodate Great Crested Flycatchers. Although the entrance hole was of sufficient size to allow use by smaller species, including the Tufted Titmouse (*Parus tylosus* Hoodey), Canadian Wren (*Troglodytes canadensis*), and Eastern Bluebird (*Sialia sialis*), the Great Crested Flycatcher was the only species that used nest boxes in large numbers (see Chapter 2). I placed nest boxes on eight nest box plots (20 nest boxes per plot) during February–March 1997. Within each plot, I placed boxes on four pine trees at 30-m intervals, alternating the heights at 1.8 m and 4.5 m above ground. All nest boxes were mounted east by southeast, as is customarily or systematically orientated as often preferred by many cavity-nesting local species (e.g., Cramer 1975, Mullin 1978, McFarlane 1982, Randall and Robinson 1994). To minimize microclimatic differences among nest boxes, I placed all nest boxes where the entrance hole would not be obscured by vegetation for >1.5 m in all directions (above, below, laterally).

In a related study, 140 nest boxes with entrances too small (3.5 cm diameter) for the Great Crested Flycatcher were placed on the same study plots during February–March 1997. These nest boxes were designed for the Tufted Titmouse and Canadian Wren. Only 4 were used for nesting during 1997/98.

Nest Box Monitoring

I visited each nest box once every 10–14 d in April and May and once every 14–21 d in June and early July. High nest boxes were reached with an aluminum extension ladder. As much as 2 hr of searching activity by Great Crested Flycatchers in a nest box, 1

monitored the nest at 2-4 d intervals. I recorded all other species that occupied nest boxes. Because flying squirrels (*Glaucomys* spp.) were not tracked from nest boxes, because flying squirrels and Great Crested Flycatchers mutually use the same nest tree cavities (pers. obs.), and I did not want to bias my comparison of nesting activities in nest boxes versus nest cavities. Because flying squirrels are also potential nest predators, I counted all squirrels observed in each nest box during monitoring visits to ensure if flying squirrel densities changed over time as a result of the nest boxes. I defined primary nest sites to be nest cavities in which flying squirrels were observed on two or more occasions within a season.

Cavity Nest Monitoring

I used standard methods (Martin and Geupel 1992) to search for Great Crested Flycatcher nests from mid April through early July, 1991-1998. Nest search efforts included a buffer strip approximately 75m wide around each study plot to ensure that birds foraging on or near the edges of plantation plots also were monitored. I visited nest search routes among plots and dual perches (early morning, late morning) to maximize comparable search effort among sites. At each site a nest was located, it was monitored regularly at 2-4 d intervals to assess nesting status (Martin and Geupel 1992, Ralph et al. 1992). Nests located <1m above ground were worked with a step ladder and the contents checked with a light and dental mirror to determine nest status. In 1992, nest cavities >1m high were searched from the ground through observation of adult behavior (e.g., carrying nest material or food into the cavity, Martin and Geupel 1992, Ralph et al. 1992, Martin et al. 1997), although some cavities in larger, more stable rings, were investigated

with Swedish-ventral interlocking ridges. In 1989, all nests >400 high were associated with a video probe inserted on a telescoping fiberoptic pole (Taylor et al., Snapper Technologies Inc., Menlo Park, California, USA). I considered nestlings to have fledged if they were alive when checked within 1 d of expected fledging and subsequent checks showed no evidence of predation or disturbance to the nest (Martin et al. 1997). I visited nest territories typically within 1–2 d after the expected time of fledging to attempt visual confirmation of the fledglings.

Statistical analyses

Analyses of nesting success included data only from years in which at least one egg was laid. In analyses of nesting success for the Great Crested Flycatcher, I used 1981 and 1982 for the length of the incubation and nesting periods, respectively (Campbell data, Taylor and Rutherford 1981). The day the last egg was laid was considered the last day of incubation. For years that I could not inspect (i.e., years very high nests in 1983), I estimated the last day of incubation through observations of parental behavior at the nest (Martin and Geupel 1993). I considered a nest to be successful if it produced >1 fledgling. I calculated nesting success rates with the Mayfield method (Mayfield 1961, 1975) as modified by Hensler and Nichols (1991). Nesting success rates for the incubation and nesting stages were calculated separately and then multiplied to determine overall success for the entire nesting period (Hensler and Nichols 1991, Hensler 1993). I tested for differences in nesting success between years and between nest types with one-tailed, standard normal Z tests (Hensler and Nichols 1991, Hensler 1993).

I used a Wilcoxon signed-rank test (SAS, 1989) to compare flying squirrel numbers on study plots between 1997 and 1998. I tested for changes in (a) the number of nest boxes occupied in primary nest sites on each plot, and (b) the maximum number of individuals occupied on each plot.

To determine if morphological differences existed between nest boxes across nest densities, I measured structural variables within circular plots centered on each nest. Within 3 m-radius (9.42 ha) circular plots, I measured percentage of bare ground, percentage of ground covered by grass, percentage of ground covered by shrubs, average shrub height, average palm-tree height, and number of saplings (stem diameter 2.5–4 cm). Within 11.3 m-radius (39.64 ha) circular plots, I measured the number of small trees (2–11 cm dbh), total basal area (m²/ha), canopy height, and maximum height. Methods for collecting habitat data follow Martin et al. (1997). Heights of nest cavities were measured with a clinometer. I used Kruskal-Wallis tests (MINITAB Inc., 1994) to compare the heights of successful and unsuccessful nest sites and maximum sapling circumference (MANCOVA) tests to compare morphological variables across nest sites. Variables recorded as percentages were $(n-1)^{-1}$ transformed before analysis.

Results

Nesting Success

During two breeding seasons, I measured a total of 39 Great Crested Flycatcher nests on study plots throughout 33 nests at nest boxes and 27 nests at nest cavities. Most nest sites (most all cavities) measured at songs by the Red-bellied Woodpecker

(*Helicoverpa virescens*) at the Northern Flounder (*Platichthys verrucosus*), but 6 (17%) were in natural habitats or reservoirs or living slash plant and turkey oak.

Twenty-four of 28 nests (85%) produced at least one offspring. Overall offspring survival was nearly identical between nest boxes (0.987 \pm 0.002) and nest study nests (0.985 \pm 0.046, $Z=0.02$, $P=0.40$). However, differences were apparent when estimates of overall nesting success were compared (Table 3-1). In 1991, nesting success was higher in nest boxes (0.933) than in oysterbeds (0.900), whereas in 1994 nesting success was better in nest boxes (0.960) than in oysterbeds (0.915, $P=0.876$, Table 3-1). Within nest study nests, nesting success did not differ between years ($P=0.14$). Within nest boxes, nesting success dropped from 57% in the first year to only 36% in the second year ($P=0.003$) due to fewer nest success during the incubation period (Table 3-2). I was unable to continue the experiment for additional years because of oysterbeds being covered in several nest-box plots during 1998-2000.

Nest boxes that were reused for a second time were more likely to fail than nest boxes being used for the first time. One of the two boxes used by Great Central Flycatchers in 1994 had been previously used for nesting either by oystercatchers or by Scaled Pigeons. Only 1 of these 6 (17%) was successful, while 5 of 14 (36%) nest boxes that had not had previous use were successful.

Nest Predation

Nest predation was the most common source of nest failure, accounting for at least 25 of 39 (64%) nest failures. Three nests failed due to disturbance (two in nest

Table 3-1: Mayfield-marking capture rates of the Great Crested Flycatcher in nest boxes and in two-catchers, Camp Mountain, Tazewell Co., 1987-1994

	n	Mean success (SD)	P
1987			
Nest boxes	13	0.333 (0.497)	0.009
Two-catchers	40	0.332 (0.487)	
1994			
Nest boxes	20	0.200 (0.400)	0.070
Two-catchers	17	0.412 (0.505)	

Table 1-3. Mayfield nesting success rates by nesting period for Great Crested Neworks using nest boxes, Camp Birding Training Site, 1997-1998

Year	Incubation period (20d)		Nesting period (15d)		Overall (20d)	
	n	Success (%)	n	Success (%)	n	Success (%)
1997	12	8.33 (66.7)	11	0.00 (0.00)	11	0.00 (0.00)
1998	30 ^a	0.44 (14.7)	18	0.00 (0.00)	20	0.00 (0.00)
	$\chi^2 = 0.001$		$\chi^2 = 0.07$		$P = 0.001$	

^a Eight (40%) of these nests were predated upon within the first 5 days of the incubation period

born in 1981, and one song in 1991). In 1981, prior to obtaining the video probe, I was unable to determine exact dates of nest failure due to nests at high tree canopies.

Documented nest predations of Great Crested Flycatchers included the nestlings flying exposed and nest failure (flycatcher probe). Flying nestlings probed on 1 Great Crested Flycatcher nests during the incubation period. In each case, the eggs were broken or missing, the nest was in disarray, and flying nestlings were observed on top of the nest, each of these nest predation events was documented only 1-2 d after the previous nest check. In addition, many depredated nests in nest boxes were described as a circular failure during the incubation period but squawks were not subsequently observed. Cowbirds probed on 2 Flycatcher nests, one containing five 12-day-old nestlings and the other containing three 12-day-old nestlings, in each case the male remained in the box for two or more days after consuming the nestlings. Although yellow warblers (*Dendroica citreolinea*), were not observed probing on Great Crested Flycatcher nestlings during the study, they were known to prey on Red-bellied Woodpecker nestlings in the study area (year class 1). Other potential, but not documented, nest predators in the study area included white throats (*Perisoreus griseus*) and Blue Jays (*Cyanocitta cristata*).

Despite the prevalence of flying squawks in nest boxes (see Chapter 2), I found no evidence that flying squawk populations increased during the course of the study. The maximum number of flying squawks counted at each plot during the peak Great Crested Flycatcher nesting season (mid-April through May) did not differ between years (Wilcoxon signed rank test, $P > 0.05$). The number of nest boxes occupied by flying

equivalents to primary nest sites during spring; nest success also did not differ between years (Wilcoxon signed-rank test, $P = 0.50$).

Nest Characteristics

High- and low-quality nest boxes were used by Great Crested Newts in similar proportions in 1990 and 1991 (Fisher's exact, $P = 1.00$). The ratio of successful to unsuccessful nests did not differ between high- and low-quality boxes (Fisher's exact, $P = 1.00$). Height of cavity nests did not differ between years (Kruskal-Wallis, $H = 0.11$, $df = 1$, $P = 0.73$) or between successful and unsuccessful nests (Kruskal-Wallis, $H = 0.01$, $df = 1$, $P = 0.92$).

Marshmallow observations around nest sites did not differ between nest boxes and tree cavities (MCMCVA, Wilks Lambda = 0.030, $P = 0.32$). I found no evidence that nest boxes selected for nesting in 1991 differed from those selected in the previous year in marshmallow reactions (MCMCVA, Wilks Lambda = 0.298, $P = 0.43$, Table 3-1).

Discussion

Nest Success vs. Nest Boxes versus Tree Cavities

I found no evidence in support of the hypothesis of nest boxes being inherently "safer" or more protected from nest predators than cavity nests. Nest predation was the most consistent cause of nest failure for Great Crested Newts in both nest boxes and in tree cavities. Although nest boxes experienced little nest predation in 1991, they were more vulnerable to egg predators in 1990. Nesting success in nest boxes decreased in

Table 2-3. Microclimate structure around nest boxes used for nesting by Great Crested Newts over a 2-yr period.

Microclimate variable	1997	1998
	(n=12)	(n=11)
Ground covered by bare soil (%)	2 (1) ^a	3 (1)
Ground covered by grass (%)	10 (4)	14 (3)
Ground covered by shrubs (%)	19 (4)	15 (3)
Stem height (m)	1.2 (0.2)	1.1 (0.1)
Foliar height (m)	0.4 (0.4)	0.1 (0.0)
No. of saplings (2.5-8.9 cm dbh) per 0.4 ha	1.0 (0.2)	2.4 (0.4)
No. of small diameter trees (0-1.5 cm dbh) per 0.4 ha	0.4 (0.0)	10.0 (3.4)
Total basal area (m ² /ha)	22.1 (2.2)	24.3 (3.1)
Canopy height (m)	18.5 (0.4)	18.7 (0.4)
Midstory height (m)	9.4 (0.4)	10.7 (0.5)

^a Mean (SE).

only 26% in 1998 because of a dramatic increase in egg predation during the incubation period (Table 3-2).

Direct evidence of nest predation by flying squirrels was confirmed for the incubation period. Although direct evidence of flying squirrel predation was limited to 3 nests, circumstantial evidence (i.e., types of disturbances to the nest) suggests that flying squirrels may have been responsible for a substantial proportion of the nest failures that occurred during the incubation period. Although others have speculated that flying squirrels are important predators on Great Crested Flycatcher nests (Langen, 1997; White and Sogard, 2000), this study is the first confirmed report of nest predation on the species by flying squirrels. Flying squirrels have been reported as predators of the eggs of other cavity nesting birds including Black-capped Chickadees (*Parus atricapillus*, Smith et al. 1984) and Red-crowned Woodpeckers (*Geococcyx borealis*; B. Conner, pers. comm., J. Kappen, pers. comm.).

Snakes are generally found to prey on cavity nests during the nesting period and not during the incubation period (Ludwig 1946, Jackson 1978, STE, Hickey and Smith 1981, Baskette and Koenig 1997). Taylor and Kammer (1993) reported two instances of predation by snakes on Great Crested Flycatcher nests, one on a nest containing 3 "heavily fledged" nestlings and one on a nest containing 2 nestlings less than 1 month old. Similarly in this study, direct evidence of nest predation by rat snakes was restricted to the nesting period. Together these data strongly suggest that snakes were not primarily responsible for the high level of egg depredation on nest boxes during the second year of the study.

Causes of Differential Nest Production in Nest Boxes versus Tree Cavities

Nest-site characteristics

Nest boxes and non-cavity nests did not differ in height or in any morphological variable that would influence nest success/failure, nor did these variables differ between years. Thus, lower nest success in nest boxes cannot be attributed to a difference in the accessibility or appropriateness of these sites to predators, either before or after nest initiation or between years. This is perhaps not surprising given the even-aged, homogeneous structure of the pine plantations.

Physical dimensions of the nest cavity did not appear to be responsible for production differences. Although I was unable to measure the size and shape of all tree cavities used by Great Crested Flycatchers, many were too high to be inspected, most cavities were old had-behind Woodpecker cavities, whose openings ranged from 3.5 to 5.7 cm in diameter (unpubl. data, Jackson 1976; Macdonald et al. 2000). Larger entrance holes have been found to affect mammalian predator access to cavity nests (Jamieson 1985a), but production rates were highest in nest boxes, which had smaller entrances (≤ 1 cm diameter) than most tree cavity nests. Obviously, temporal differences in nest production in nest boxes were not influenced by cavity entrance size because all boxes had the same size entrance hole.

Dispersible loads are sometimes thought to be greater in older nest sites. Supporting evidence for the effect of dispersible loads on nest success is equivocal, with some studies finding dispersible loads and nesting success negatively correlated (Moller 1990, Robner et al. 1994, Urpy and Hogg 1997) while others finding no relationship (Haggen

et al. 1994, Bondell and Verboek 1996, Davidson et al. 1997). Regardless, winged nest birds could not account for the differences in nest success in nest boxes during the current year, because (1) nest boxes were thoroughly cleaned of nesting debris in the intervening winter (2) the majority of nest failures occurred because of predation on eggs (3) nestboxes attract predators.

Because flying squirrels nest and den in cavities, I assessed whether the availability of nest boxes increased the density of flying squirrels. Any increase in squirrel densities would increase the odds of a squirrel opportunistically encountering and robbing a flycatcher nest. However, the numbers of flying squirrels using nest boxes did not change between years. Moreover, squirrels occupied the same number of nest boxes each year, indicating an increase in the movement of squirrels among nest boxes in 1998. Squirrels not using nest boxes were not counted, but reported use of nest boxes is likely correlated with the total density of squirrels on study plots because of the large number of boxes unoccupied by flying squirrels (Chapter 2).

Potential for learning by nest predators

Several researchers have demonstrated a positive correlation between the risk of nest predation and the age of a nest site, both within (Stokun et al. 1987) and among (Johnson and Le 1992, Martin 1992) cavity-nesting bird species. Species and individuals that experience new nest success have lower rates of nest predation than non-experiencers, but rely on old evidence for nest sites. One of the mechanisms behind this pattern is that nest predation may be more significant at the locations of older nest sites. Previous studies have shown that nest predation by mammals increases with the age of a nest box,

For example, Kohnstein and Riedel (1989) found that nest success of Tree Swallows (*Iridoprocne bicolor*) as nest house decreased over time because of increasing predation by raccoons (*Procyon lotor*) and cat snakes (*Elaphe carolinensis*), which are important nest predators in Southeastern Illinois, have been shown to develop long-term spatial memory for the locations of nest houses used by House Wrens (*Troglodytes aedon*) (Giesert 1993a,b, 1999). In Sweden, nest boxes for Goldfinches (*Carduelis arvensis*) that were preysed on in a given year tended to be preysed on in successive years (Jönvall and Fänge 1943).

In this study, predation on eggs increased dramatically during the second year of the study. Nest boxes that were reused by Great Crested Flycatchers were less likely to be successful than nest boxes being used for the first time. These results support the hypothesis that nest predation in this study involves explicit nest boxes as a prey resource, likely through the development of long-term spatial memory. It is unlikely that much stage development was the mechanism, given that only a small proportion of the available nest boxes was occupied (see Methods: Nest boxes; also Chapter 2).

Moreover, predation intensity on failed nests placed in nest boxes (after the conclusion of this study) were higher in nest boxes that had been previously used by Great Crested Flycatchers than in nest boxes that had no previous nesting attempts (Appendix 4a).

Using cameras, Forrester and Ratten (2008) documented flying squirrels and males entering to deposit Wind Thrush (*Aphelocoma maculosa*) nests several days after the original predation event. Such observations suggest that a variety of nest

predators are capable of lowering the biomass of profitable prey sizes and returning preferentially to them. Although flying squirrels were probably responsible for most predation on eggs in 1998, rat snakes also may have played a role. Taylor and Karasov (1991) observed a small (14 cm in length) rat snake taking a Great Crested Flycatcher nestling from a nest less than days after another nestling had disappeared from the same hole. They speculated that the snake made return visits to the nest because of anomalously small size.

Summary and Conclusions

This study demonstrates that nest boxes were not necessarily safer sites than nest cavities. My results also underscore the importance of looking at the temporal dynamics of nest predation, as static comparisons of nest success between natural sites and nest boxes may give incomplete or misleading results. If years were pooled in this study, then one would have concluded that Great Crested Flycatchers had identical nesting success in nest boxes and nest cavities. Worse yet, if one had drawn conclusions after only one year of study, then the conclusion would have been that Great Crested Flycatchers have reduced nesting success when breeding in nest boxes. Many researchers fail to report sexual differences in nest success and/or nest predation in nest boxes (e.g., Espadaño 1984, Nilson 1984, Rabinov and Adkinson 1992, Powell et al. 1997), which may weaken their conclusions about nest boxes. Other researchers present evidence that nest predation increases over time at nest boxes, without discussing the ecological significance of this pattern (e.g., Bellrose et al. 1986, Dwyer et al. 1999). When researchers

understand comparisons of breeding ecology in nest boxes versus tree cavities, it is essential that they report sexual changes in these parameters.

Theoretical and empirical evidence indicates that nest predation may increase with the age of a nest box. The predatable „permanent“ locations of nest boxes may actually make them more vulnerable over the long-term to nest predators than tree cavities (Isenrod 1945 vs. 1989–1993). Further research is needed to identify the factors – including type of predator (opportunistic vs. snails vs. owls), availability of alternative prey in the study area, persistence rates of natural nest cavities in the study area – that determine how nest predators will respond to nest boxes. For example, predation by snakes in Boreal Owl nests appears to be influenced by the abundance of alternative prey, as a study area with low rates of nest predation (3%) and abundant alternative rodents, Korpimäki (1997) found little relationship between nest box age and predation rates by snakes. Researchers should take advantage of the opportunity to use nest boxes to study mechanisms of nest predation and their relevance to avian life history theory – I predict that, within a given area, nest predation rates in nest boxes will tend to be higher than those in tree cavities when the cavities in the area are relatively short-lived (i.e. they do not persist as long as the nest boxes) and the nest predators in that area are sufficiently reliant on bird eggs and nestlings as an important part of their annual diet.

To conclude that reproductive parameters obtained from nest box studies are not representative of birds nesting in tree cavities (Moller 1999) is to ignore the spatial and temporal variation that exists everywhere in nature. “Tree cavities” are not one static set of idealized conditions. Cavities used by a given species can vary considerably within a

study were or were not major in their field (age, religion, hairiness, structural integrity, susceptibility to predators, and so forth) because of which they were. Nest boxes are useful tools that allow the manipulation of many of these factors in controlled experiments, thus facilitating the study of particular mechanisms or ecological relationships that otherwise would be difficult or nearly impossible to study (Kenny et al. 1991). The use of nest boxes as ideally designed experiments to study nest predation and its relevance to avian life history theory should be increased rather than decreased.

CHAPTER 4
LIFE HISTORY TRAITS IN CAVITY-NESTING BIRDS:
WHY IS NESTING SUCCESS GREATER
IN EXCAVATORS THAN IN NON-EXCAVATORS?

Introduction

Cavity-nesting birds can be separated into two groups of species based on their nesting behavior: species that typically excavate their own nest cavities in (usually) dead wood (i.e., excavators), and species that do not excavate their own nest cavities (i.e., non-excavators) and depend instead on natural holes or those created by excavators. Traditionally, studies that have compared aspects of nesting ecology from a life history perspective have grouped all cavity-nesting bird species into a single nest type (Lock 1974, 1988, Miao 1993, Riebeloh 1999) or have focused only on non-excavators and included their life history traits in all cavity nesters (Nilsson 1984, 1986). However, Li and Martin (1991) studied a suite of excavator and non-excavator songbirds coexisting in time and space and demonstrated that non-excavators suffered higher nest failure than did excavators. Martin and Li (1991) suggested that life history traits vary systematically between excavators and non-excavators, with excavators generally having greater nest success, smaller clutch sizes, longer nesting periods, and fewer brood attempts per year.

In Jackson, Li, and Martin (1994) found that non-excretors (1) nested at lower heights, (2) had greater nest concealment, (3) used older nest cavities, and (4) tended to have smaller body size than excretors. Li and Martin (1991) reasoned that each of these factors would afford nest predators increased access to the entire nestcup ability to immediately potential detection of the nest, but these assumptions were not formally investigated. Moreover, since these factors were all inter-correlated in their study, making it difficult to distinguish which factor was more important than others. For example, nests that were lower were also more concealed by secondary vegetation.

Predator pressure and other environmental conditions can vary across habitats. Nesting success can vary among different habitats, each with different nesting substrates, different rates of nest predation, as well as different cavity-nesting bird species. I report here the results of a study of nesting success and other life-history traits for a suite of important and a suite of non-excretor songbirds in managed pine forests of the Southwestern Coastal Plain. My objectives were (1) to confirm the proposed pattern of differential nest success and nest predation between excretors and non-excretors, and (2) to assess the importance of environmental correlates that have been suggested as decreasing differential nest success.

Methods

Study Site

I conducted my research at Camp Blending Training Site, a Florida Army National Guard facility encompassing approximately 20,000 ha in the north of Clay County, Florida. My field assistant and I searched for nests of cavity-nesting birds as a

young stands dominated by slash pine (*Pinus elliotii*), plantations (young aged, 25–40 years old) interspersed with longleaf pine (*P. palustris*) stands (mature-aged, with a significant component of >40 year-old trees). Most nest searching was focused on twelve 10-ha plantation study plots, one 8-ha plantation study plot, and one 18-ha plantation with scattered patches of turkey oak (*Quercus laevis*; see Chapter 3 for a detailed description of plantations). Unidentifiable woody species were generally absent in mature oaks and usually limited to scattered turkey oak saplings in dense younger oaks. Shrubs, which rarely exceeded heights of 1–1.5 m (see Table 3-1), included cane palmetto (*Savanna exoniifolia*), gallberry (*Illex glabra*), and other woody species.

Horizontal nest patches of cavity-nesting birds in the study area included in oaks (*Dryopteris* spp.), southern flying squirrels (*Glaucomys volans*) and other small mammals (e.g., *Peromyscus gambelii*), muskrat houses, and crows (*Corvus brachyrhynchos*, *Cyanocitta cristata*, *Amazona*, *Corvus*, *Geococcyx*).

Nest Searching and Monitoring

My field assistants and I used standard field methods (Martin and Geupel 1993) to search for cavity-nest trees and birds through early July of 1994–1998. I searched nest search sites in plantations among plots and old periods (early morning, late morning) to maintain comparable search effort among years. I monitored nests regularly at 3–4 day intervals in years during which Martin and Geupel (1993, Ralph et al. 1993). Nests located <100 above ground were checked with a step ladder and the contents checked with a light and forest access to determine clutch size and nest status. During 1994–1997, nest cavities 1–1 m high in dead trees (snags) were monitored from the ground through

observation of adult behavior (e.g., sampling and statistical or trend tests for carry). Martin and Gangel (1985, Balpin et al. 1993, Johnston et al. 1997), although some crevices in logs, more mobile snags were investigated with Swedish sectional tree-climbing, isolates. In 1998 investigations of the high were conducted with a video probe mounted on a telescoping aluminum pole (TreeTop II, Bardsper Technologies, Inc., Menlo Park, California, USA). Eastern snags were monitored systematically in 1993 while establishing study plots and those that also are included in analyses.

I did not actively search for nests of the Carolina Wren (*Phoenicurus ruber*) because it was a "back-and-forth" species in the study area, nesting in areas with potential brood or nest cavities in brush piles, trees, and shrubs.

Determination of Clutch Size, Nesting Period, and Nest Success

I determined clutch size for nests that were accessible by ladder or by video probe. I used published information (Marston 1970, Anderson 1970, Grant 1982, Eischen et al. 1988, Taylor and Karstner 1991, Weidner et al. 1992) to estimate the length of the incubation and nesting periods for each species. I estimated site-specific values for these parameters as I reported nest success by ladder and by video means.

The day the last egg in a clutch was laid was considered the first day of incubation for all species except for Eastern Screech-Owls (*Otus asio*), which were monitored as a one-by-one basis regarding its laying and incubation behavior. For species that I could not inspect (e.g., some high snags from 1996-1997) I estimated the first day of incubation through observations of parental behavior in the nest (Martin and Gangel 1985). I considered a nest to be successful if it produced ≥ 1 fledgling. Unsuccessful nestings re-

have changed if they were alone when checked) within 10 of expected fledging and subsequent checks showed no evidence of predation or disturbance to the nest (Martin et al. 1997). I visited nest territories typically within 1-2 d after the expected date of fledging to attempt visual confirmation of the fledglings.

I calculated daily survival rates for the incubation and nesting stages with the Mayfield method (Mayfield 1961, 1971) as modified by Hessler and Pyle (1987). Because daily survival rates for the two stages did not differ for any species (standard survival Z test, $P > 0.01$, Appendix B, Hessler and Pyle (1987), Hessler 1982), I calculated a single daily survival rate for the entire nesting cycle and used that to determine overall nesting success for each species.

Nest site Selection

For each nest site, I recorded nest species and condition and measured nest height with a clinometer. I measured nest concealment at nest sites in 1993 by estimating the percentage of the nest obscured by vegetation from a low vantage in the marsh, near, south and west of the nest at nest height (Martin et al. 1997). I identified tree canopies from reconnaissance aerial cavity-survey throughout the course of the study and identify the relationship between cavity age and nest success. When possible, cavity dimensions were measured to assist in identifying the source (i.e., *Ardea herodias* species) of cavities.

Statistical Analysis

I used chi-square analysis and multiple-comparison methods to program CONTAG (Hosmer and Lemeshow 1989) to test for differences in daily survival probabilities

among species. I compared mean clutch size for incubators and non-incubators with Mann-Whitney tests (MINITAB (ver. 1996)).

I determined the relationships among nest success rates, nest height, and body mass with Spearman's correlation coefficients; rank correlation coefficients were used because I did not a priori expect to assume that relationships between variables would be linear. Body mass estimates were obtained from Dawson (1993). Where species, nest height of successful and unsuccessful nests was compared with Mann-Whitney tests. In some cases, Red-bellied Woodpeckers made >1 nesting attempts at a given nest site within the same year; in these cases, I included only the outcome of the first nest in analyses of nest heights versus nest success.

Results

Clutch Size and Nesting Phenology

I found a total of 119 nests of 11 cavity-nesting bird species (summed across all Table 4-1). Clutch size was determined at 18 (15%) of these nests. Mean clutch size was lowest (1.8) for the Red-bellied Woodpecker and highest (4.5) for the Carolina Chickadee and Great Crested Flycatcher (Table 4-1). Clutch size averaged across species was 4.24 ± 0.71 (SD) for incubators and 4.20 ± 0.71 for non-incubators (Mann-Whitney, $P = 1.00$).

Double-brooding was common for Red-bellied Woodpeckers and Downy Woodpeckers, with Red-bellied Woodpeckers commonly laying their second clutch in the same cavity within the first year. I could not confirm double-brooding by any other species.

Table 4.1. Mean (range) clutch size, typical number of broods, and duration of incubation and nesting periods for 11 species of cavity-nesting birds

Species	Clutch size	No. broods	Incubation (d)	Nesting (d)
Examiners				
Red-bellied Woodpecker <i>Melanerpes carolinus</i>	3.6 (2-5)	2	12	21
Downy Woodpecker <i>Picoides pubescens</i>	4.3 (3-5)	1	12	21
Hairy Woodpecker <i>Picoides villosus</i>	— ^a	1	12	28
Northern Flicker <i>Colaptes auratus</i>	6.5 (3-10)	1	12	25
Carolinian Chickadee <i>Parus carolinensis</i>	6.9 (4-10)	1	12	18
Brown-headed Nuthatch <i>Sitta pygmaea</i>	4.5 (4-5)	1	14	18
Non-examiners				
Wood Duck <i>Aix sponsa</i>	—	—	—	—
Eastern Screech-Owl <i>Otus asio</i>	3.3 (2-4)	1	26	25
Great Crested Flycatcher <i>Myiarchus cinerascens</i>	4.8 (3-6)	1	14	12
Tufted Titmouse <i>Baeolophus bicolor</i>	4.6 (4-5)	1	14	18
Eastern Bluebird <i>Sialia sialis</i>	5 (5)	2	14	18

^a Insufficient data.

although it is possible that the Tuffed Titmouse occasionally joined two broods. On one occasion I observed a Tuffed Titmouse feeding a nest 150 m from an earlier successful nest, but Great Crested Flycatchers occupied the nest before I could confirm if the same pair of parents was involved. The possibility also exists that some Red-bellied Woodpeckers may have managed to nest a third brood very late in the season, but nest searching and monitoring during August was outside the scope of this study.

Nesting Success

Mayfield estimates of nest success were generally higher for excavator species than for non-excavator species, although there was considerable overlap between the two groups (Table 4-2). Mean nesting success (\pm SD) averaged across species with ≥ 5 nests was 67% (range: 41–83%) for 5 excavator species and 48% (range: 33–63%) for 4 non-excavator species (Table 4-2, Mann-Whitney, $P = 0.10$). Daily survival rates of excavators did not differ from daily survival rates of non-excavators ($\chi^2 = 2.44$, $df = 1$, $P = 0.12$).

Daily survival rates did not differ among excavators ($\chi^2 = 5.62$, $df = 1$, $P = 0.21$) but differed significantly among non-excavators ($\chi^2 = 8.39$, $df = 1$, $P = 0.002$) because of the low nest survival rates of the Great Crested Flycatcher and Eastern Bluebird relative to the Eastern Screech-Owl (Table 4-2). Daily survival of Eastern Screech-Owl nests (0.89 \pm 0.03) was significantly greater than that of Great Crested Flycatcher nests (0.66 \pm 0.04, $P = 0.004$). Daily survival was not significantly greater for Eastern Screech-Owl nests than for Eastern Bluebird nests (0.82 \pm 0.04, $P = 0.129$) because of the large variance associated with the Bluebird survival estimate.

Table 4-1. Number of successful gone out of town nests, number of days nests were observed, daily survival rates (SD) and Mayfield nest success estimates for 11 species of cavity-nesting birds, Crops (Standing Timber Site) 1995-1998

Species	Observations			Mayfield	
	Successful / Total	days	Daily survival (SD)	nest success	
Eucalyptators					
Red-bellied Woodpecker	73 / 100	2 491	0.9993 (0.0013)	68.4	
Downy Woodpecker	29 / 35	482	0.9912 (0.0088)	74.7	
Hairy Woodpecker	0 / 1	8	0	—	
Northern Flicker	2 / 3	17	0.9848 (0.0152)	56.8	
Carolina Chickadee	14 / 25	347	0.9933 (0.0067)	48.6	
Brown Banded Nuthatch	11 / 14	308	0.9869 (0.0131)	62.8	
Non-eucalyptators					
Wood Duck	0 / 1	5	0	—	
Eastern Screech-Owl	5 / 7	227	0.9912 (0.0088)	62.8	
Great Crested Flycatcher	19 / 44	709	0.9847 (0.0153)	78.3	
Tufted Titmouse	11 / 34	159	0.9748 (0.0252)	49.6	
Eastern Bluebird	1 / 4	67	0.9848 (0.0152)	71.5	

Table 4-3 Causes of nest failure for each survey nesting species.

Species	Cause determined			Cause unknown ^a	Total
	Pre-laid	Failed	Other ^b		
Excavators					
Red-Bellied Woodpecker	7	2	6	13	28
Downy Woodpecker	3	0	0	3	6
Hairy Woodpecker	0	0	0	1	1
Northern Flicker	1	0	0	0	1
Carolin Chickadee	7	2	1	1	11
Brown-headed Nuthatch	0	0	1	2	3
Total	18	4	8	20	50
Non-excavators					
Wood Duck	1	0	0	0	1
Eastern Screech-Owl	1	1	0	0	2
Great Crested Flycatcher	10	1	0	4	15
Tufted Titmouse	3	1	0	0	4
Eastern Bluebird	0	1	1	1	3
Total	22	4	1	5	32

^a Cause unknown could not be estimated for many cases of nest failure.^b Other natural causes of nest failure, including nest abandonment and disease.

Causes of Nest Failure

Nest predation was the most common cause of nest failure (Table 4-3), accounting for 48 of 84 (58%) nest failures, 78% of all nest failures for which the cause was determined. Nest predation accounted for a higher proportion of nest failures among non-incubators than among incubators ($\chi^2 = 4.45$, $df = 1$, $P = 0.04$). Among non-incubators, 87% of all nest failures were attributed to nest predation.

Confirmed nest predators included the cane toads (*Xenopus laevis*), yellow rat snake (*L. olivacea*), and northern flying squirrel. Without resources at hand, I was unable to document the relative importance of these predators. However, some important observations can be made. Rat snakes were observed preying on nestlings in 2 Great Crested Flycatcher nests and nestlings in 1 Red bellied Woodpecker nests. Flying squirrels were known to have preyed upon at least 2 Great Crested Flycatcher nests during the incubation period. In both instances, flying squirrels or their nest material were observed on top of the bird nest ~2 days after the previous nest check. One Carolina Chickadee nest suffered extensive physical damage to the cavity wall possibly indicative of a larger mammalian predator. In addition, 1 Downy Woodpecker nest was lost to other species of woodpeckers. A multi-billed Woodpecker stayed in Downy nest during the egg-laying period, and Red bellied Woodpeckers depredated 1 Downy nest during the hatching period.

Failure from nest items being supplied or broken by wind and rain was more common for incubators than for non-incubators (Table 4-3). Eight of 30 (26%) failed

incubator nests were lost from tree fall, whereas only one of the 34 (3%) failed nests of tree incubators was lost to tree damage (Fisher's exact, $P = 0.877$).

Post-nest behavior and nesting success

Species and condition of nest-leave

Most nest sites were located in pine ranges (Table 4-4). Nest types were alkali pine (40%), longleaf pine (31%), turkey oak (19%), and other pine species (10%). The Brown-headed Nuthatch, Carolina Chickadee, and Eastern Bluebird nested mostly in pine trees and avoided oak trees. As a group, non-incubators tended to nest in oak trees more frequently than did incubators (Table 4-4), probably because of the availability of natural hollows in live (and dead) oak trees.

Nest concealment

Data collected from a sample of nests in 1977 indicated that nest concealment was not a factor in this open forest system. (Less than 1% of the empty nests contained leafy vegetation concealing the nest.) Thus, if concealment measurement of nest concealment is independent of nest

Nest height

Nest heights of successful nests were significantly greater than nest heights of unsuccessful nests for the Red-bellied Woodpecker, Eastern Screech Owl, and Downy Woodpecker (Table 4-5). Nest heights were not different for the Downy Woodpecker. Small samples in one or both of the most numerous categories precluded meaningful statistical tests for most other species; for example, I had only 3 failed nests of the Tufted Titmouse.

Table 4-4. Frequency (%) of tree condition types and tree species shown the most stress by cavity-nesting birds (percent with ≥ 3 nests included). Percentages calculated separately for tree condition and for tree species.

Species	Tree condition			Tree species	
	Living	Dead portion of live tree	Live dead	Forest	Oak
Excavators					
Red-bellied Woodpecker	99	1	0	99	0
Downy Woodpecker	91	3	6	83	18
Northern Flicker	100	0	0	67	33
Carolina Chickadee ^a	100	0	0	95	5
Brown-headed Nuthatch	100	0	0	100	0
Average	99	1	0	87	13
Non-excavators					
Eastern Screech Owl	100	0	0	10	90
Coastal Redstart	79	6	15	63	37
Tufted Titmouse	47	33	40	40	60
Eastern Bluebird	100	0	0	100	0
Average	84	8	24	68	32

^a Does not include four additional nests placed in hollow live oaks.

Table 4-3. Median nest heights at successful and unsuccessful nests for 8 cavity-nesting species, Camp Blending Training Site, Florida, 1993-1999.

	Successful	Failed	<i>P</i> ¹
Expendables			
Red-bellied Woodpecker	10.4 (24)	1.6 (16)	0.002
Downy Woodpecker	10.2 (17)	16.3 (4)	---
Northern Flicker	9.0 (2)	10.9 (1)	---
Carolinian Chickadee	1.0 (14)	1.4 (11)	0.16
Downy-headed Nuthatch	2.4 (20)	4.9 (3)	0.71
Nonexpendables			
Eastern Screech-Owl	2.8 (2)	1.2 (2)	0.040
Great Crested Flycatcher	7.5 (18)	2.9 (15)	0.002
Tufted Titmouse	4.4 (11)	3.9 (3)	0.36
Eastern Bluebird	2.9 (3)	1.2 (3)	---

¹ One-tailed Mann-Whitney test of the hypothesis that Failed nest heights < Successful nest heights.

Correlations among nesting success, nest height, and body mass

Comparing nest success, there was a positive correlation ($\phi_{\text{NS}} = 0.46$, $P = 0.007$) between nest nest height and nest nest success (Table 4-4), and this relationship appeared to be linear (Fig. 4-1). Species with the lowest nest nest heights (e.g., Carolina Chickadees, Eastern Bluebirds) had lowest nest success. There were no other significant correlations among these variables (Table 4-4).

Cavity origin and age

Care monitoring of nest cavities in successive years allowed identification of the source of nest cavities used by cavity-nesting birds (Table 4-5). Excavation revealed that over nest holes, except for a sample of excavations in which large woodpeckers occupied the majority of smaller woodpecker species and enlarged them for their own use. Red-bellied Woodpeckers provided more cavities for non-excavators than did any other excavator species. A clear relationship was especially apparent between the Red-bellied Woodpecker and the Great Crested Flycatcher (Table 4-5), if Red-bellied Woodpecker cavities were still intact a first second year and not used by the woodpeckers, then they usually were occupied by Great Crested Flycatchers. Carolina Chickadees cavities were used by several species, especially the Eastern Bluebird.

Red-bellied Woodpeckers that raised the nest nest tree for a second year were less successful than Red-bellied Woodpeckers that nested in a newly excavated cavity, peeling years, (but including second broods), 37 of 54 (70%) nest attempts in new excavations were successful compared to 3 of 18 (16%) nest attempts in 1-year old excavations (Fisher's exact, $P = 0.007$).

Table 4-6 Spearman's correlation coefficients between nesting success, nest height, and body mass of each species. Significance levels indicated as follows:

	Nesting success	Nest height (m)	Body mass (gm)
Nesting success	—	$\rho = 0.88$ $\rho < 0.001$	$\rho = 0.84$ $\rho < 0.001$
Nest height		—	$\rho = 0.87$ $\rho < 0.001$
Body mass			—

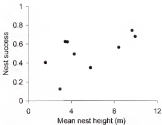


Figure 4.1 Relationship between mean nest height and nesting success estimates for 9 species of cavity nesting birds: Camp Blending Training Site, Florida, 1971-1993.

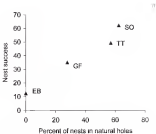


Figure 4-2 Relationship between percentage of nests built in natural holes (x = those not excavated by other birds) and nesting success for 4 species of bee-eaters (EB = Eastern Bluebird, GF = Green-Crowned Flycatcher, TT = Tailed Tanager, SO = Sooty Tern) Owl, Ceryle, Hanging Tanager, Florida, 1995-1998

Three non-excavators – the Eastern Screech-Owl, Great Crested Flycatcher, and Tuffed Titmouse – made minimal use of 'natural holes' (i.e., interstices not generated by other birds; Table 4-7). Natural holes included clefts/bark and hollow branches in oak trees, the natural hollow formed between shelled pine cones, and also peckholes formed on decaying stumps. I did not observe any of these natural holes being used for nesting in consecutive years. One of natural holes was previously occupied ($n = 1$ EG) with nesting success rates for non-excavator species, and this relationship appeared to be loose (Fig. 4-2).

Discussion

Nest Success of Excavators and Non-Excavators

Excavators generally had greater nest success than non-excavators, but this difference was not significant because of the large overlap between the two groups (Table 4-2). For example, the Eastern Screech-Owl – a non-excavator – had greater nest success than two excavators – the Carolina Chickadee and the Northern Flicker. Within the family Paridae, the non-excavator (Tuffed Titmouse) had greater nest success than the excavator (Carolina Chickadee).

This finding contrasts with the distinct delineation between excavators and non-excavators documented in Arizona by Li and Martin (1991) and Martin and Li (1992), the only other studies to compare nesting success of cavity-seeking birds occupying in time and space. In their work, nest success was close to approaching 100% for several woodpecker species, and there was almost no overlap between the two groups. Nest success for 8 excavator species averaged 80% (range, 63-100%) and for 8 non-excavator

species averaged 60% (range 37-70%, Li and Martin 1991). Sample sizes of nests in their study were comparable to those in mine, Martin and Li (1993) had ± 7 nests for a third of the cavity-nesting species in their study, and I had ± 7 nests for a third of the species in my study.

Nest success rates documented in my study area were usually lower than those reported from other localities for the same species (Li and Martin 1991, Solomon and Korman 1994, see Appendix C). For example, Mayfield nest success of the Carolina Chickadee was lower in my study area (41%) than in Illinois (60%, Johnson 1992) or in a nest box study in Tennessee (70%, Potts 1998). Nesting success for Eastern Bluebirds in my study area (37%) was lower than my study in the literature, my sample of nests was small, but even when nesting attempts in nest boxes in the study area were included (61% of total nesting attempts), Mayfield nest success was still <60% (unpubl. data).

Nest predation appears to be higher in my study area than in many others (Appendix C). One possible explanation for relatively low nest success in Florida pine plantations is site-specific differences in the density and diversity of nest predation. Direct evidence is lacking to conclude that the density of nest predators is higher in southern pine forests than in other plant communities in North America because its most studied the densities of nest predators are not known nor are their populations fluctuating measured. However, there are certainly more species of snakes in the southeastern United States than in many other regions of the country, including high-diversity snake forests in Arizona (Behler and King, 1978, Smith and Riddle 1982). Two southeastern species (the rat snake [*E. obsoletus*] and pine snake [*E. gramineus*]) are especially important as predators on bird nests, including nests in tree cavities (e.g., Johnson 1979, 1984, 1978,

Largent 1993, Phillips and Cook 1993, also see Chapter 3). Moreover, evidence indicates that this Red-bellied Woodpecker (*Picoides borealis*) evolved the behavior of drilling up wells around its nest cavity as an adaptation to reduce predation by the sympatric red necks (Jackson 1978, Reddy et al. 1990, MacFarlane 1992). Red necks are excellent climbers and spend most of their time in trees (R. Fries, pers. comm.).

Thus, although this study confirmed that nest excavators have higher nest success than nest non-excavators, the pattern was strikingly weaker than that documented in high elevation forest slopes in Arizona (Le and Martin 1998, Martin and Le 1992), where cavity nesters experienced lower levels of nest predation.

Additional research is needed to determine if high nest predation rates are typical of Florida pine forests. Within my study area, Red-bellied Woodpecker nest success rates did not differ between young slash pine plantations and older longleaf pine stands (unpubl. data), indicating that high nest predation is not restricted to young pine plantations.

Evaluation of Overlapping Hypotheses About Differential Nest Success

Nest height

If predation pressure selects for higher nests, then successful nests should be higher than those that are unsuccessful. In this study, nest height and nest success were positively related across species. However, within individual species, successful nests were higher than failed nests for some species but not for others (Table 4-3). Thus, evidence for the nest-height hypothesis was mixed. Similarly, Le and Martin (1992) found a strong relationship between nest height and nest success when comparing nests

values across species but did not find significant relationships within any species. Closer examination of this pattern suggests that the range of nest heights used for nesting, together with the species of nest predator or predators, determines whether successful nests are higher than failed nests for a given species.

An explicit assumption is that nest height mostly reflects horizontal exposure, but this has yet to be demonstrated experimentally for specific mammalian nest predators. However, a variety of evidence suggests that a threshold of vulnerability exists for cavity nesters, with nests <2 m in height being used vulnerably to incidental mammalian predators. For example, Albano (1990) found that most chickadee nests (>1 25 m in height) were destroyed and the cavity walls damaged, presumably by terrestrial mammals such as raccoons (*Procyon lotor*), opossums (*Didelphis virginianus*), and striped skunks (*Melephias erpionus*). Similarly, Randall and Robertson (1997) found depredated Tree Shrews (*Dactylopsila lineata*) nests averaged 1.8 m in height while successful nests averaged 4.5 m in height. Nilsson (1984) found that nests <2 m above ground were more likely to be preyed upon than higher nests for 3 species of cavity nesters, but found no such relationship for 3 other cavity-nesting species, one of which suffered nest predation mostly from arboreal woodpeckers.

Many birds are likely to maintain a rich guild of antipredators of varying body sizes and diverse foraging modes. Pillitteri et al. (1990) argued that the stark nests of Northern Cardinals (*Cardinalis cardinalis*) are subject to a rich guild of nest predators and high overall levels of predation, features which combine to minimize predictably safe nest sites; they argued that this explains the lack of influence of nest-site variables such as height or concealment on the outcome of predation (Coxson et al. 1988; Pillitteri et

et al. 1994). A variety of nest predator species was present in my study area, including two snake species that are constant threats. Predator species richness combined with high overall levels of nest predation may reduce the strength of selection for safe cavity nests in isolated pine forests. Supporting evidence comes from the work of Soren (1999), who found that mean height of successful and unsuccessful nests did not differ for Red-tailed Woodpeckers or Downy Woodpeckers in two longleaf pine forests in northern Florida.

It is also important to note that if the dominant nest predators in a given system are ground predators (e.g., crows, woodpeckers), then low nests would be safer than higher nests. The nest height hypothesis assumes that nest predators are predominantly terrestrial and have greater difficulty finding and/or accessing higher nests than lower nests. There are important assumptions that need to be substantiated.

Nest concealment

The predictions of the nest concealment hypothesis were not supported by my data. The only nests that were partially obscured by branches of vegetation were those of the Carolina Chickadee – an insectivore species with short nest lengths of 1.6 m.

Traditionally, dense foliage near open-top nests is thought to reduce predation by concealing the nest from discovery (e.g., Martin 1990), presumably by visually-oriented nest predators. Increased foliage density may reduce the risk of nest discovery by concealing the nest (Nolan 1976, Murphy 1981, Westmoreland and Best 1982), reducing the movement of predators (Bouwes and Brown 1984) or increasing the number of possible exit than a predator used to enter (Martin and Roper 1984). The idea that dense foliage would have the opposite effect on cavity nests (i.e., increased nest predation) appears to have been developed by Fuller-Lake and Pomeroy (1964) who found Brown

When nests surrounded by sparse vegetation had lower nest predation than nests surrounded by dense vegetation. They speculated that dense vegetation could allow *Geothlypis trichas* to see and destroy (a phenomenon that is actually interspecific competition not predation) to approach nests more easily without being seen, but they did not observe this occurring. Although their work has been cited by others (e.g., Finch 1988, Li and Martin 1991) as evidence that predators have better access to cavity nests when they are concealed, this phenomenon has yet to be documented. Moreover, if concealment of the nest by vegetation is beneficial for open-cup nesters but not for cavity nesters, then it follows that nest predation must use different cues to find open-cup and cavity nests, a concept for which there is also no evidence.

I found no evidence that Carolina Wrens destroyed or usurped cavity nests, contrary to the prediction by Lead et al. (1985) that competition from wrens would be a major source of nest failure for secondary cavity-nesting birds in pine plantations. In fact, Carolina Wrens rarely used tree cavities or nest sites formed by placing their own nests into cracks and crevices or brush piles and palmetto fronds.

Nest cavity age

Nest predation and the age of a nest site were positively correlated, both across and within cavity-nesting bird species. Nest excavator species that made use of natural holes had greater nest success than those which would excavate. Similarly, Louiberg and Akinin (1992) found that nest predation rates for Pied Blythbirds (*Pardaliparus hypoleucus*) nests were significantly higher in old woodpecker cavities than in natural hollows formed in hardwood trees by branch fall and decay. These holes were abundant

in their study area, their such natural holes would have had less previous nesting activity than such woodpecker holes, which, by definition, had always had previous bird use.

Among Red-bellied Woodpeckers, those that reused their nest cavities in successive years had lower nest success than those that excavated new cavities each spring. Hillman et al. (1991) found the same pattern for Black Woodpeckers (*Dryocopus americana*). Among Great Crested Flycatchers, birds using older nest boxes suffered higher nest predation than those using new nest boxes (see Chapter 1), which constitutes further support for the hypothesis that cavity age is correlated with predation risk. In summary, I found a variety of evidence that new excavators have relatively low nest success because nest predators learn over time to exploit older nest sites as a prey resource.

Body size

Body size was not correlated with nest success in this study. Predator rates on cavity nests were inversely correlated with the species' body size (Dunn 1977, Li and Martin 1981) but Hillman (1984) found the opposite result. In addition to body size, other factors (e.g., aggressiveness, mobbing behavior, vigilance) probably influence a species' effectiveness at detecting or repelling would-be nest predators.

Conclusions

Cavity-nesting birds had lower nest success in the young, regenerating pine forests of southeast Florida than in other locations in North America. Although nest excavators had greater nest success than most non-excavators, the pattern was not so clear

as in the phalaropus-pint (P. phalaropus)-terns studied by La and Martin (1991), upon which much life history theory about cavity-nesting birds has been based (Martin and La 1992). High levels of nest predation combined with the relatively low heights of cavity nests in a young, expanding forest may have masked the differences between the two nest types in my study.

This study provides additional evidence for the importance of cavity size (i.e. predation exposure) and nest height as factors determining differences in life history traits of cavity-nesting birds. Because these two factors frequently may be correlated, manipulative experiments to simultaneously address these factors would provide further insight into their relative importance and how they might interact in different situations.

Nevertheless, the tight relationship between nest size of the Red-bellied Woodpecker and Great Crested Flycatcher provides strong support for the hypothesis that cavity size may be of primary importance in determining lower nest success (and consequently higher annual reproductive effort; Martin and La 1992) in non-extractors. Close monitoring of individual females over a 3-yr period indicated that non-extractors used excavated nest sites as soon as they were created. Great Crested Flycatchers were highly dependent on the cavities excavated by Red-bellied Woodpeckers (Table 4 Pg. 1) even observed a few instances where Red-bellied Woodpeckers and Great Crested Flycatchers used the same nest cavity sequentially within the same season. Predation risk increased in successive years within a given nest site, even though nest concealment and nest height obviously did not change over time.

My results also underscore the importance of looking at local and regional differences in nest predation. In most studies, the identity of nest predators is unknown

but, identification of nest predators from nest remains is not a reliable technique.

Larriere (1984) and a variety of nest predators may respond differently to nest height. More research is especially needed on the ecology of tree-climbing snakes in southern pine forests.

Although it may be appealing to focus on interspecific interactions (i.e., nest predators) to explain nest site selection of forest birds, it is equally important to recognize the importance of within-specific interactions as a component of cavity-nesting birds (i.e., interference competition for nest cavities, commensalism between non-exclusives and excluders). A simple explanation for the greater vulnerability of non-exclusives to nest predators is that non-exclusives must be more opportunistic in their choice of nest sites, particularly if they are more reliant on woodpecker-excavated cavities. As nest trees decay, they become progressively shorter and thus the highest cavities are the first to disappear, leaving lower cavities available. Under this scenario, nest predators must necessarily be selective foragers, because nest-site selection is determined only by the pattern of age and decay in the cavity resource and the consequent scramble for resources based on body size and sexual dimorphism. Nilsson (1984) found that smaller cavity-nesting birds were forced to nest lower in the presence of other species. As commensals, non-exclusives are forced to accept the cavities that are available, including old woodpecker cavities that have an increased risk of nest predation.

CHAPTER 3 CONCLUSIONS AND SYNTHESIS

Synthesis

Non-accrator are likely to be most-site limited in the young pine forests that dominate the Southeastern Coastal Plain, because cavity density is positively correlated with tree density, tree age, and the abundance of hardwood species (see Balon et al. 1944, Waters et al. 1980). However, habitat quality may set an upper limit on the suitability of a given area for breeding birds. For example, the densely wooded slash pine plantations I studied appeared to be marginally suitable as breeding habitat for Eastern Bluebirds (*Sialia sialis*), thus, producing population increases regardless of the number of cavities that became available. Most areas of early-serotiny species, including Eastern Bluebirds and Great Crested Flycatchers, are characterized by microhabitats with many snags, low density of trees, and a partially open canopy (open-pole state, Miller 1980), all features that were rare in these plantation study plots.

I found that non-accrator species that were released on cavities in snags were most likely to be most-site limited, whereas those that were opportunistic or using natural cavities and serotons (e.g., Carolina Wren, *Troglodytes aedon*) were not most-site limited (Chapter 2; Brown and Balon 1982). Use of a variety of cavity types also was

correlated with nest success for a given species, probably because these rates had less precision due to nesting levels (Chapter 4).

Martin and Lu (1992) suggested that spatial and temporal variability in the quantity and quality of nest sites could drive increased reproductive effort by nest excavation (e.g., larger clutch sizes, more failed attempts per year) as an evolutionary context. However, contrary to Martin and Lu (1992), I found no significant differences in clutch size or daily nest survival rates between excavators and non-excavators (Chapter 4). Clearly, site-specific factors are also at play, and these life history relationships need further exploration.

Nest predation rates on cavity nests were higher in my study area than for similar species in other locales (see Appendix C). I found a variety of evidence supporting the importance of cavity use as a determinant of nest success. Species that are able to nest in a variety of natural holes had greater nest success than those that relied predominantly on old woodpecker cavities that had been used by birds in the previous year. Egg deposition around trees used by the Great Crested Flycatcher (*Myiarchus cinerascens*) increased during the second year nest boxes were available, evidence presented in Chapter 3 indicated that non-hole nesting resulted in nest predators learning the locations of nest boxes or developing search images for them.

Finally, prescribed burning seemed to facilitate the discovery and use of nest boxes by secondary cavity-nesters in this study. From a management perspective, if increasing cavity-nesting bird populations is a management goal in fire-managed pine

forests, managers may find that the addition of nest boxes to newly forested areas will result in the highest local densities of cavity-nesting birds.

Research Needs

Community-level studies of avian nest success have become common in many regions of the United States during the last 5–10 years, providing insight on the impacts of timber management practices, habitat fragmentation, and landscape design on populations of both open cup-nesters and cavity-nesters, and Neotropical migrant species and resident species. However, this type of information is still unknown in Florida, a state that already has lost >90% of its original coverage of longleaf pine (Diers 1983). Research on avian nest success in the longleaf pine ecosystem has been restricted to two local species: the Red-cockaded Woodpecker (*Picoides borealis*) and Pileated (*Colinus virginianus*). My study is the first to measure nest-site selection and nesting success of a community of cavity-nesting birds in southern pine plantations. It is difficult to fully interpret my findings because of the lack of similar information from older, less intensively managed pine forests in the Southeast. Comparative studies of avian reproductive success in different forest types and landscapes should be a priority for future research in Florida. Future research in Florida should focus on nest-site selection, nest predation, and nest parasitism – topics that are still almost-completely unstudied in forested landscapes in Florida.

Pred predation have been sufficiently studied, especially in southern pine forests. From a management perspective, additional research is needed on how nest predation can

affected by site management. Foremost is the need for further research on the ecology of the resident flying squirrel as it uses site components and nest profiles, both in pine plantations and in longleaf pine barrens and woodlands. Previous studies have achieved mixed, but generally negative, results of management activities designed to control the impact of flying squirrels on cavity systems (Conner and Ruckelsh 1991, Conner *et al.* 1994, Meebold *et al.* 1995).

Avian ecologists also need a better understanding of the ways that different nest-profile types are to locate cavity nests. Although I found support for the concept that larger nests are less conspicuous and/or less accessible to nest predators (Chapter 4) and for the concept that cavity age is positively correlated with predator risk (Chapters 3-6), carefully designed manipulative experiments are needed. These scientific strategies are usually not available (Ba and Myster 1997), and thus, they form a set of unresolving hypotheses that are best addressed with factorial experiments (Quinn and Keough 1993). Nest boxes are likely to be an accurate tool for testing some of these relationships between nest predators and nest-site selection for cavity nesting birds.

LITERATURE CITED

- Abrahamson, W. G., and D. C. Hansen. 1960. Pine Chickadees and their parasites. Pages 183-195 in R. L. Myers, and J. J. Sweet, editors. *Ecoscience of Florida*. University of Central Florida Press, Orlando, Florida, USA.
- Akaike, H. Y., A. Carlson, and A. Lindberg. 1988. Nest cavity size and clutch size of Post-Opuntia: *Parus-like* breeding in natural cavities. *Oikos* 53:217-229.
- Allen, B. J. 1982. Nesting mortality of Carolina Chickadees breeding in natural cavities. *Condor* 84:371-381.
- Baker, J. L., and F. W. King. 1978. *The Audubon Society Field guide to North American reptiles and amphibians*. Alfred A. Knopf, New York, USA.
- Bewerley, S. R., and E. R. Bacher. 1992. Sustainable harvesting of parrots for conservation. Pages 79-115 in S. R. Bewerley and M. F. R. Sargent, editors. *New World parrots in crisis: solutions in conservation biology*. Smithsonian Institution Press, Washington, DC, USA.
- Bellrose, J. C., and J. Pomeroy. 1988. Nesting success and nest site preferences in House Wrens. *Condor* 90:403-409.
- Delaney, P. C., R. L. Johnson, and T. V. Meyer. 1994. Relative value of natural cavities and nesting boxes for Wood Ducks. *Journal of Wildlife Management* 58:661-676.
- Dohy, C. J., M. D. Strepp, and D. A. Hill. 1990. *Red-capped technology*. Academic Press, London, UK.
- Dock, C. B., and J. F. Lynch. 1978. Breeding bird populations of natural and suburban wooded forests in the Santa Monica. *Condor* 80:182-191.
- Brown, G. B., and L. D. Hartz. 1988. Effects of spatial heterogeneity on ground-nest dependence. *Journal of Wildlife Management* 52:869-873.
- Brown, J. D., and R. F. Eakin. 1983. Population biology of cavity nesters in southern Arizona: do nest sites limit breeding abundance? *Condor* 85:61-71.

- Brown, J. D., R. Tanselman, and R. E. Brown. 1984. Nest and observation of cavity nesting birds at central Missouri. North-Central Forest Experiment Station, Research Note NC-214. St. Paul, Minnesota, USA.
- Brath, T. 1945. Cavity use by secondary cavity nesting birds and response to manipulations. *Condor* 47:461-468.
- Cady, M. L. 1985. An introduction to habitat selection in birds. Paper 3-86 in M. L. Cady, editor. *Habitat selection in birds*. Academic Press, Orlando, Florida, USA.
- Cannon, E. N. 1975. Occupancy of entrances to woodpecker nest cavities. *Auk* 92:233-234.
- Cannon, E. N., and D. C. Rudolph. 1973. Effects of territory selection and sharing on Red-cockaded Woodpecker cavity tree clusters. *Wildlife Society Bulletin* 21:41-49.
- Cannon, E. N., M. E. Anderson, and J. G. Dickson. 1984. Relationships among territory size, habitat, song, and nesting success of Northern Cardinals. *Auk* 101:23-31.
- Cannon, E. N., D. C. Rudolph, D. Brown, and E. R. Schaefer. 1986. Red-cockaded Woodpecker nesting success, desert predators, and nest-site flying squirrels in Texas. *Wilson Bulletin* 98:697-703.
- Cox, J. 1947. The Breeding Bird Survey in Florida 1945-1946. *Florida Field Naturalist* 17:26-48.
- Daniels, A. H. H., and B. Schlander. 1967. The effect of interspecific nest location on the breeding biology of the Forked-bill Tree Toad *Amphibia*. *Ibis* 129:115-128.
- Dennis, J. W. 1983. A comparative study of Florida woodpeckers in the non-breeding season. M. S. Thesis. University of Florida, Gainesville, USA.
- Dow, H., and S. Fudge. 1945. Breeding and nest dispersal of the Goldeneye, *Amphalia clangula*. *Journal of Animal Ecology* 12:465-479.
- Dugger, R. H., D. D. Dugger, and L. B. Fredrickson. 1977. Annual survival rates of female Hairy Woodpeckers and Wood Ducks in southeastern Missouri. *Wilson Bulletin* 111:3-4.
- Dunn, E. 1977. Predation by vesper sparrowhawks on breeding blue (Pipilo spp.) in relation to the density of the individuals. *Journal of Animal Ecology* 46:403-412.

- Dunning, J. B., Jr. 1993. *CRC handbook of avian body masses*. CRC Press, Boca Raton, Florida, USA.
- East, M. L., and C. M. Forney. 1988. The effect of mowburn on breeding populations of birds in broadleaf temperate woodlands. *Bird* 130:593-600.
- Elorisk, P. R., D. S. Dolken, and D. Whyte. 1988. *The birder's handbook: a field guide to the natural history of North American birds*. Simon and Schuster, Inc., New York, USA.
- Estabrook, M. W., and W. D. Koenig. 1993. Gopher snake attraction to birds nests. *Southwestern Naturalist* 37:259-260.
- Evanson, A., and B. Sjögren. 1992. Effects of the introduction of *Pterodroma* (Florida) *Agelaius* on the composition of a permanent bird community. *Oikos* 64:45-55.
- Engstrom, R. T. 1993. *Avian-perturbations in Florida habitats: analysis and control*. Florida Game and Fresh Water Fish Commission. Nongame Wildlife Program Final Report, Tallahassee, Florida, USA.
- Farrerworth, G. L., and E. A. Silvers. 2000. Observations of Wood Thrush nest predation in a large coniferous forest. *Wilson Bulletin* 112:87-87.
- Filmer, T. L., R. Bostwick, and P. M. Hedley. 1994. Predation on Northern Cardinal nests: does choice of nest site matter? *Oecologia* 96:760-764.
- Fitch, D. M. 1989. Relationships of nesting system habitat to nest-box use and reproductive outcomes in House Wrens. *Condor* 91:848-859.
- Frost, C. C. 1993. Five examples of changing landscape patterns in the longleaf pine ecosystem. Pages 37-47 in: E. M. Pimenton, editor. *Proceedings Tall Timbers Fire Ecology Conference No. 13: The longleaf pine ecosystem: ecology, restoration and management*. Tall Timbers Research, Inc., Tallahassee, Florida, USA.
- Geddes, P. R. 1996. Nest-box versus natural-cavity nests of the Eastern Screech-owl: an interdisciplinary study. *Journal of Raptor Research* 33:156-157.
- Greeney, P. A., and J. H. Pimm. 1986. *Extinction/Quarrel*. In A. Fitch, and F. Gill editors. *Birds of North America*, No. 341. Academy of Natural Sciences, Philadelphia, USA, and American Ornithologists Union, Washington, DC, USA.

- Deble, T. C. and F. F. Fursethor. 1994. Tuffed Titmouse. In A. Poole, and F. Gill, editors. *Field of North America*, No. 60. Academy of Natural Sciences, Philadelphia, USA, and American Ornithologists' Union, Washington, DC, USA.
- Newton, H. G., Jr. 1989. *Ecological experiments: purposes, designs, and execution*. Cambridge University Press, Cambridge, UK.
- Parker, R. E. and D. C. Gayen, Jr. 1980. Song Sparrow in managed stands of the South Carolina Coastal Plain. *Southern Journal of Applied Forestry* 7:224-229.
- Rams, L. D. and P. C. Fredericks. 1990. The role of the Endangered Species Act in the conservation of biological diversity: an assessment. Pages 25-48 in J. Cairns, Jr. and T. V. Crowder, eds. *Integrated environmental management*. Lewis Publishers, Inc., Chelsea, Michigan, USA.
- Richard, H. E. 1975. *A field guide to birds' nests*. Houghton Mifflin Co., Boston, USA.
- Roeder, G. L. 1985. Estimation and comparison of biasness of daily nest survival probabilities using the Mayfield method. Pages 789-806 in R. J. T. Morgan and P. H. North, editors. *Statistical ornithology*. Springer-Verlag, New York, USA.
- Roeder, G. L. and J. D. Nichols. 1988. The Mayfield method of estimating nesting success: a model, extensions, and confidence limits. *Wilson Bulletin* 91:42-51.
- Stearns, E. C. and E. G. Smith. 1988. Eastern Bluebird responses to structural modification and perches. *Wilson Bulletin* 91:482-483.
- Thom, J. E. and J. E. Sauer. 1989. Program CONTRAST: a general program for the analysis of survival or recovery rate estimation. *Fish and Wildlife Technical Report 26*. U.S. Department of the Interior Fish and Wildlife Service, Washington, DC, USA.
- Tipton, D. and D. Jackson. 1994. *Rare vertebrate survey of Camp Maunabo Trapping Site*. Final Report of Florida Natural Areas Inventory/The Nature Conservancy to Department of Military Affairs, Florida Army National Guard, St. Augustine. Florida Contract 6987004-91-4-0019.
- Watts, B. L. 1995. Composition of bird communities following stand replacement fires in western Rocky Mountain conifer forests. *Conservation Biology* 9:1590-1600.
- Watts, B. L., S. M. Pomeroy, and P. Hensley. 1988. A flood-rainfall event model for northwestern bird banding service use. *Auk* 105:993-1002.

- Inglis, D. F. 1965. Nesting phenology and comparisons for nest-site usage, Red-headed and Red-bellied Woodpeckers and European Starlings. *Auk* 82:109-117.
- Jackson, J. A. 1970. Predation of a black rat snake on yellow-shafted Flicker nestlings. *Wilson Bulletin* 82:327-330.
- Jackson, J. A. 1974. Gray rat snakes versus Red-cockaded Woodpeckers: predation-prey relationships. *Auk* 91:343-347.
- Jackson, J. A. 1976. How to determine the status of a woodpecker nest. *Living Bird* 15:329-339.
- Jackson, J. A. 1977. Notes on the behavior of the Gray Rat Snake [*Elaphe obsoleta* (synonym)]. *Journal of Mississippi Academy of Science* 22:64-66.
- Jackson, J. A. 1978. Predation by a gray rat snake on Red-cockaded Woodpecker nestlings. *Bird-Banding* 49:147-148.
- Jackson, J. A. 1988. The woodpeckers past, present, and in the future past, present, and future. Pages 115-139 in J. A. Jackson, editor. *Bird Conservation*. University of Wisconsin Press, Madison, USA.
- Jones, F. C., R. F. Johnston, H. O. Wilson, G. J. Munn, and W. J. Bealman. 1984. The Smithsonian study of the Wood Thrush. *American Naturalist* 124:17-30.
- Johnson, L. E., and L. E. Kumpf. 1984. Nesting success of cavity-nesting birds using natural tree cavities. *Journal of Field Ornithology* 55:36-51.
- Koenig, W. D., P. A. Grewy, and J. L. Dickinson. 1992. Buses, buses, and budgets: confounding factors in experimental manipulations in ecological studies? *Oikos* 63:360-364.
- Koppeko, J. 1984. Clutch size and breeding success of Tengmalm's Owl (*Aegolius funereus*) in natural cavities and nestboxes. *Ora Fennica* 41:69-83.
- Koppeko, J. 1987. Selection for cavity hole shape and factors of breeding success in Tengmalm's Owl (*Aegolius funereus*). *Journal of Animal Ecology* 56:343-356.
- Korol, K. J., and B. J. Stern. 1995. Bird use of natural and artificial nestboxes during winter. *Wilson Bulletin* 107:243-250.
- Kruuse, M., and A. Kikkas. 1992. Nest predation and breeding success in Common Tawnyshrike nesting in human and natural cavities. *Ora Fennica* 69:7-12.

- Leck, D. 1958. The natural regulation of annual numbers. *Charendon* Oxford, UK.
- Leck, D. 1968. Ecological adaptations for breeding in birds. *Methuen*, London, UK.
- Leck, D., W. B. Maron, and T. E. Martin. 1989. Song variability and song timing: birds in shrub pine plantations. *Journal of Wildlife Management* 53:1349-1371.
- Leighton, W. B. 1991. Great Crested Flycatcher (*Myiarchus cinerascens*). In A. Poole, and F. Gill, editors. *Field Guide to North America* 9th. 388. Academy of Natural Sciences, Philadelphia, USA, and American Ornithologists' Union, Washington, DC, USA.
- Lorenzen, E. 1999. Random why predation cannot be inferred from nest predation. *Oikos* 100:704-708.
- Lucas, A. B. 1948. Stable dependence of bird nests. *Wilson Bulletin* 58:217-218.
- Li, P., and T. E. Martin. 1991. Nest-site selection and nesting success of cavity-nesting birds at high elevation forest denudage. *Auk* 108:603-618.
- Longfellow, A., and E. W. Chickadee. 1992. The pied flycatcher. T. & A. D. Poyser, London, UK.
- Mappes, T. J. Mappes, and J. Kotze. 1994. Experimenters, nest-site choice and breeding success in the pied flycatcher. *Oecologia* 98:142-149.
- Martin, T. E. 1991a. Nest predation and nest-site site perspectives on old patterns. *Parasitica* 43:125-132.
- Martin, T. E. 1991b. Evolutionary determinants of clutch size in cavity-nesting birds: nest predation or limited breeding opportunities? *American Naturalist* 137:117-134.
- Martin, T. E., and G. B. Gysel. 1990. Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* 61:583-599.
- Martin, T. E., and P. Lu. 1981. Life history traits of open- vs. cavity-nesting birds. *Ecology* 72:279-292.
- Martin, T. E., and J. J. Roper. 1988. Nest predation and nest-site selection of a western population of the forest thrush. *Oikos* 52:51-57.
- Martin, T. E., C. B. Paine, C. J. Casing, W. M. Hochstetler, F. Allen, and W. Jackson. 1997. BIRD field protocol. *Montana Cooperative Wildlife Research Unit*, University of Montana, Missoula, USA.

- Mayfield, R. 1961. Nesting success calculated from exposures. *Wilson Bulletin* 73: 223-234.
- Mayfield, R. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456-460.
- McCauley, W. C., S. A. Benary, S. M. Kieffer, and N. D. Cox. 1986. Song sparrows in Florida: are they sufficient for average populations of primary cavity-nesters? *Wildlife Society Bulletin* 14: 46-48.
- McClint, S. M. 1978. Nest site and population demographics of White-breasted and Pinyon Nuthatches. *Condor* 80: 343-352.
- McFarlane, R. W. 1992. *A witness in the pines: the ecology of the Red-cockaded Woodpecker*. W. W. Norton & Co., New York, USA.
- Miller, K. R. 2000. Nest site selection and nest-site location of cavity-nesting birds in Florida pine plantations. (Abstract.) Page 126 in Abstracts of The Wildlife Society 7th Annual Conference, The Wildlife Society, Bethesda, Maryland, USA.
- Millroy, P. A., J. A. Goss, D. E. Baskin, and S. T. Crockett. 1990. Setting priorities for the conservation of fish and wildlife species in Florida. *Wildlife Monographs* 112.
- MSNTAS Inc. 1994. MSNTAS Software Manual, Release 11 for Windows. State College, Pennsylvania, USA.
- Minshall, L. R., L. D. Carley, and C. B. Chandler. 1999. Effects of nestbox flying squirrels on nest success of red-cockaded woodpeckers. *Journal of Wildlife Management* 63:536-545.
- Moller, A. P. 1989. Parasites, predators and nest boxes: facts and statistics in nest box studies of birds? *Oikos* 56: 421-429.
- Moller, A. P. 1998. Effects of parasitism by a haematophagous mite on reproduction in the house wren. *Ecology* 79:2150-2157.
- Mosley, M. T. 1945. Nest success and nesting habits of Eastern Kingbirds and other *Tyrannidae*. *Condor* 47: 208-219.
- Meyers, R. L. 1990. *Scrub and high pine*. Pages 130-193 in R. L. Meyers, and J. J. Grier, editors. *Ecosystems of Florida*. University of Central Florida Press, Orlando, Florida, USA.

- Newson, J. 1979. Population ecology of sparrows. T and A. D. Poyser, London, UK.
- Newson, J. 1984. The role of nest sites in limiting the numbers of hole-nesting birds in avian. *Biological Conservation* 75:263-279.
- Newson, J. 1993. Population limitations on birds. Academic Press, San Diego, California, USA.
- Now, M. M. 1957. Nesting success in altricial birds. *Auk* 74:305-321.
- Nilsson, S.-G. 1975. Clutch size and breeding success of birds in nest boxes and natural cavities. *Var Population* 24:209-213.
- Nilsson, S.-G. 1988. The evolution of semi-able selection among hole-nesting birds: the importance of nest predation and competition. *Oikos* (Supplement) 33:165-175.
- Nilsson, S.-G. 1994. Evolution of hole-nesting in birds: an balancing selective pressure. *Auk* 113:432-435.
- Nilsson, S.-G., E. Johann, and M. Tjornberg. 1991. Is avoidance by black woodpeckers of old nest holes due to predators? *Animal Behaviour* 41:429-440.
- Nolan, Y. 1978. The ecology and behavior of the Prairie Warbler (*Dendroica discolor*). Ornithological Monograph No. 26. American Ornithologists' Union, Washington, DC, USA.
- Now, R. F. 1989. Longleaf pine and woodpecker and logskunk components of an oak-pine forest ecosystem. *Natural Areas Journal* 9:211-213.
- On, L. 1988. An introduction to statistical methods and data analysis. Third edition. Pitman Publishing Co.-Boston, USA.
- Parryman, B. G., J. E. Smith, and W. A. Link. 1989. The 1994 and 1995 occupancy of the North American breeding bird survey. *Bird Populations* 7:44-61.
- Phillips, L. P., Jr., and K. E. Gash. 1993. Predators of Red-cockaded Woodpecker young in a cypress-swamp. *Florida Field Naturalist* 21:47-49.
- Pollock, B. C. 1976. The use of nest cavities by nesting Eastern Bluebirds. *Journal of Wildlife Management* 40:555-563.
- Pollock, B. C. 1977. Breeding adaptations in the Eastern Bluebird. *Condor* 79:339-342.

- Pin, T. D. 1986. Reproductive biology of Cassin's Chickadees. *The Auk* 103: 19-194.
- Pinckell, R. L., J. Verner, and L. W. Gregg. 1957. A comparison of the breeding ecology of birds nesting in houses and tree cavities. *Auk* 74: 646-674.
- Quinn, J. F., and A. E. Dunham. 1983. On hypothesis testing in ecology and evolution. *American Naturalist* 122: 403-417.
- Sakaguchi, L. D., M. Muehlen, Y. M. Buckley, and P. Arcese. 1997. A long-term study of the breeding success of Eastern Bluebirds by year and cavity type. *Journal of Field Ornithology* 48: 7-18.
- Salyt, C. J., G. R. Gangel, P. Pyke, T. B. Mather, and D. P. DeGarin. 1993. *Handbook of field methods for measuring birdbeaks*. General Technical Report FWS-OCS-144. Pacific Southwest Research Station, U.S. Forest Service, Albany, California, USA.
- Snyder, M. G., and M. White. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. *Wildlife Monographs* 95: 1-66.
- Snyder, W. B., and R. J. Robertson. 1984. Cavity-to-forest succession and nest-site use by secondary hole-nesting birds. *Journal of Field Ornithology* 45: 27-33.
- Snyder, W. B., and H. A. M. Verboek. 1986. Old nest material in nest boxes of Tree Swallows: effects on reproductive success. *Condor* 88: 142-152.
- Sponsoring, R. W., and R. P. Labisky. 1983. Effects of semi-aged timber management on bird colonization of the tropical-pine forest in north Florida. *Journal of Wildlife Management* 49: 1089-1098.
- Stearns, B. A., O. Ogilvie, and P. Chivers. 1993. Effect of nest-site quality on reproduction in Great Tits. *Journal of Animal Ecology* 62: 755-769.
- Stoddard, E. E. 1945. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* 9: 1-48.
- Stout, F. M., H. Brock, and W. Zinner. 1978. *Swainson's Doves and Swainson's Thrasher: Redbreasted Woodpeckers (Amphisp. bairdii) (C. J. This Greatful)*. *May* 34: 37-45.
- Robertson, R. J., and W. B. Snyder. 1990. A comparison of the breeding ecology of a secondary cavity-nesting bird, the Tree Swallow (*Iridoprocne bicolor*), in nest boxes and natural cavities. *Canadian Journal of Zoology* 68: 1266-1282.

- Birdsall, D. C., H. Kyle, and E. H. Couser. 1990. Red-tailed Woodpeckers vs. red jacks: the effectiveness of the cross-burner. *Wilson Bulletin* 102:14-22.
- SAS Institute, Inc. 1987. SAS/STAT guide for personal computers, Version 6.12. SAS Institute, Inc., Cary, North Carolina, USA.
- Beane, J. R., and S. Driggs. 1986. Recent population trends of the Eastern Bluebird. *Wilson Bulletin* 102:234-252.
- Brown, J. P. L. 1988. Use of nest boxes by Eastern's Chickadees: nesting success and effect on the breeding population. *Wildlife Society Bulletin* 16:123-132.
- Scott, J. M., and F. L. Ramsey. 1981. Length of court period as a possible source of bias in estimating nest success. *Studies in Avian Biology* No. 6:409-412.
- Scott, M. A., J. L. Luskewich, and M. P. Moulton. 1990. Effects of overabundance on nest box selection and annual productivity of eastern Starbirds (*Sialia sialis*) in northeastern Georgia. *Texas Journal of Science* 40:71-82.
- Shackelford, C. E., E. E. Brown, and E. H. Couser. 1988. Red-tailed Woodpecker (*Melanerpes formicivorus*) In A. Poole and F. Gill, editors. *Birds of North America*, No. 105. Academy of Natural Sciences, Philadelphia, USA, and American Ornithologists' Union, Washington, DC, USA.
- Short, L. L. 1981. Woodpeckers of the world. Delaware Museum of Natural History Monograph No. 4, Doverville, Delaware, USA.
- Slater, G. 1990. Brown-headed Nuthatches and Eastern Bluebirds in southern Florida pinehills: breeding biology, nest-site selection, and the influence of habitat on nesting success. M. S. Thesis. University of Florida, Gainesville, USA.
- Smith, H. H., and E. D. Sinker, Jr. 1981. Raptors of North America: a guide to field identification. Golden Press, New York, USA.
- Somerset, D. A. 1985a. Role of nest predation in three species of hole nesting birds: influence on choice of nesting habitat and reproductive behaviour. *Oikos* Scandinavia 48:261-269.
- Somerset, D. A. 1985b. Nest hole drill in *Tingitida s. Del.* *Agelaius phoeniceus* as defence against nest predation involving long-term occupancy in the predator. *Journal of Animal Ecology* 54:179-192.
- Somerset, D. A. 1989. Reduced predation by great horned owls on nests of *Tingitida s. Del.* in simulated forests. *Animal Behaviour* 37:832-843.

- Sargent, G. A. 1992. Reduced predation by nest (and broodling) differential effects on *Troglodytes (Ore) virens* and artificial nests. *Oikos* 63:268-273.
- Smith, M. A., M. E. Gashner, and P. S. Axel. 1949. Interactions of southern flying squirrels, *Glaucomys volans*, and cavity-nesting birds. *Canadian Field-Naturalist* 137:461-480.
- Snuffer, D. F., and L. B. Best. 1940. Nest-site selection by cavity-nesting birds of dynamic habitats in Iowa. *Wilson Bulletin* 54:505-507.
- Stadel, D. W. 1961. Territorial and breeding habits of Red-bellied Woodpeckers. *American Midland Naturalist* 74:115-119.
- Steen, D. 1999. Nest site selection and nesting success of three woodpecker species in north Florida longleaf pine forests. M. S. Thesis. University of Florida, Gainesville, USA.
- Taylor, W. K., and M. A. Gashner. 1956. Breeding biology of the Great Crested Flycatcher in central Florida. *Journal of Field Ornithology* 42:28-39.
- Thomson, J. W., R. G. Anderson, C. Hays, and E. L. Ball. 1979. Sinks. Pages 42-47 in J. W. Thomson, ed., *Wildlife habitats in managed forests—the Blue Mountains of Oregon and Washington*. U. S. Forest Service, Agricultural Handbook, No. 333. U. S. Government Printing Office, Washington, DC, USA.
- Urey, T. M., and G. R. Hogg. 1987. Frequency of nest tree maintenance: effects on Wood Duck nesting in South Carolina. *Journal of Wildlife Management* 51:881-887.
- van Balen, J. H., C. J. H. Bury, J. A. Staddon, and E. R. Gorchs. 1982. Spikes-on hole-nesting birds in natural nest sites. I. Availability and occupation of natural nest sites. *Auk* 99:1-20.
- van Heesterdonck, L. 1937. Adaptation to hole-nesting birds. *Evolution* 11:358-367.
- van Heesterdonck, L. 1970. Population dynamics. Pages 211-425 in D. S. Farner and J. B. King, editors. *Avian biology*. Vol. 1. Academic Press, New York.
- Waser, J. R., B. R. Noon, and J. Verner. 1990. Lack of nest-site limitation in a cavity-nesting bird community. *Journal of Wildlife Management* 54:329-345.
- Westmacott, D. and L. B. Best. 1940. The effect of disturbance on blue-winged Green nesting success. *Auk* 103:776-780.

- Wade, D. H., and J. T. Segstad. 2008. Nest box use and productivity of Great Crested Flycatchers in prescribed burned longleaf-pine forests. *Journal of Field Ornithology* 79: 147-152.
- Watts, S. C., and G. E. Woolfenden. 1973. Breeding of the Eastern Starling in central Florida. *Bird-Banding* 44: 118-125.
- Wilson, C. W., B. E. Masters, and D. A. Pollock. 1993. Breeding bird responses to post-grassland occupancy restoration for Red-cockaded Woodpeckers. *Journal of Wildlife Management* 57: 55-67.
- Wolcott, H., D. A. Clarkin, and D. Hanesy. 1999. *Woodpeckers: a guide to the woodpeckers of the world*. Houghton Mifflin Co., Boston, USA.

APPENDIX A

RELATIVE ABUNDANCE OF BIRDS IN SLASH PINE PLANTATIONS
CAMP BLANDINO TRAINING SITE, FLORIDA, 1999-2000

Appendix A. Relative abundance of birds at each pine plantation, Camp Blending Training Site, Florida, 1980-1998. Birds were surveyed at 70 permanent point counts (relative birds times per year between April and June ($n = 344$ total point count visits)). The ten most abundant species are as follows:

Common name	Scientific name	Total Counts ^a	Frequency ^b
		Number (N)	(%)
Academe sp.	<i>Academe sp.</i>	1 (<1)	<0.1
Red-shouldered Hawk	<i>Buteo lineatus</i>	1 (<1)	0.01
Wild Turkey	<i>Meleagris gallopavo</i>	4 (<1)	0.02
Northern Redstart	<i>Colinus virginianus</i>	1 (<1)	0.04
House Finch	<i>Zonotrichia querula</i>	9 (3)	0.12
Yellow-bellied Cuckoo	<i>Coccyus americanus</i>	6 (8)	0.08
Eastern Screech Owl	<i>Otus asio</i>	6 (8)	<0.01
Great Horned Owl	<i>Bubo virginianus</i>	6 (8)	<0.01
Barn Owl	<i>Bubo varia</i>	6 (8)	<0.01
Common Nighthawk	<i>Chordeiles um</i>	1 (<1)	<0.01
Chickadee	<i>Parus carolinensis</i>	7 (<1)	0.01
Red-bellied Woodpecker	<i>Melanerpes formicivorus</i>	61 (10)	0.48
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	8 (8)	<0.01
Downy Woodpecker	<i>Parus pubescens</i>	56 (8)	0.14
Red-bellied Woodpecker	<i>Parus carolinensis</i>	2 (<1)	0.02
Mountain Flicker	<i>Colaptes auratus</i>	1 (<1)	0.01
Pileated Woodpecker	<i>Dryocopus pileatus</i>	4 (<1)	0.02
Woodpecker sp.	---	6 (8)	0.01

Appendix A Continued.

Common name	Scientific name	Total Counts Number (%)	Frequency (%)
Eastern Wood Pewee	<i>Contopus virens</i>	1 (<1)	<0.01
Great Crested Flycatcher	<i>Myiarchus cinerascens</i>	179 (88)	0.88
White-eyed Vireo	<i>Vireo griseus</i>	18 (9)	0.15
Yellow-throated Vireo	<i>Vireo flavifrons</i>	3 (<1)	0.03
Red-eyed Vireo	<i>Vireo olivaceus</i>	1 (<1)	0.01
Blue Jay	<i>Cyanocitta cristata</i>	44 (2)	0.18
American Crow	<i>Corvus americanus</i>	12 (1)	0.19
Palm Crow	<i>Corvus sinuatus</i>	0 (0)	<0.01
Crow	<i>Corvus sp.</i>	0 (0)	<0.01
Carolina Chickadee	<i>Parus carolinensis</i>	36 (1)	0.06
Tufted Titmouse	<i>Baeolophus bicolor</i>	39 (4)	0.44
Brown-headed Nuthatch	<i>Sitta pusilla</i>	15 (1)	0.09
Carolina Wren	<i>Troglodytes aedon</i>	78 (8)	0.88
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>	21 (2)	0.08
Eastern Bluebird	<i>Sialia sialis</i>	4 (<1)	0.03
Wood Thrush	<i>Geothlypis trichas</i>	0 (0)	<0.01
Gray Catbird ¹	<i>Dumetella carolinensis</i>	9 (1)	0.02
Brown Thrasher	<i>Toxostoma rufum</i>	1 (<1)	0.01
Northern Parula	<i>Parula americana</i>	9 (<1)	0.02

Appendix A. Continued

Cresson name	Scientific name	Total Counts Number (%)	Frequency (%)
Pink Warbler	<i>Dendroica pinus</i>	227 (34)	0.63
Common Yellowthroat	<i>Geothlypis trichas</i>	33 (5)	0.18
Hooded Warbler	<i>Plicaria citrea</i>	8 (0)	0.01
Summer Tanager	<i>Piranga rubra</i>	48 (4)	0.32
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	158 (32)	0.45
Indigo Bunting	<i>Junco phoeniceus</i>	4 (0)	0.02
Northern Cardinal	<i>Cardinalis cardinalis</i>	88 (6)	0.41
Brown-headed Cowbird	<i>Molothrus ater</i>	14 (1)	0.02
Total ^a		1,297	

^a Total number of birds counted within 1 km radius of the observer

^b Proportion of total point count visits during which the species was recorded at any distance from the observer

^c Uncertain breeding status, potential breeder but very few birds seen after April

^d Does not include wintering migrants recorded occasionally in mid-April. Sub-
represented Kinglet (*Regulus satrapa*) - Cedar Waxwing (*Merula migratoria*),
Black-throated Blue Warbler (*Dendroica cerulea*), Yellow-rumped Warbler (*D.
coronata*), Palm Warbler (*D. palmarum*), American Goldfinch (*Carduelis tristis*)

APPENDIX B

MONITORED DAILY SURVIVAL RATES OF CAVITY-RESTORING BRIDS
AT EACH STAGE OF THE MISSING CYCLE

Appendix 3. Differences (2-tailed Z tests) in Mayfield daily survival rates (SD) at each stage of the nesting cycle: Camp Blending Training Site, Florida, 1983–1988

Species	No. nests	Daily survival rate (SD)		Z
		Incubation period	Nesting period	
Excavators				
Red-bellied Woodpecker	18	0.8816 (0.0010)	0.7917 (0.0006)	1.095
Downy Woodpecker	25	0.9530 (0.0050)	0.7897 (0.0044)	0.760
Hairy Woodpecker	1	0	0	—
Northern Flicker	3	1.0000 (0.0000)	0.4793 (0.0204)	1.050
Carolinian Chickadee	23	0.9424 (0.0011)	0.9823 (0.0044)	-1.743 *
Green-headed Nuthatch	14	0.9747 (0.0077)	0.9022 (0.0077)	-0.907
Non-excavators				
Wood Duck	1	0	0	—
Eastern Screech-Owl	7	0.9673 (0.0127)	0.9952 (0.0047)	-0.463
Great Crested Flycatcher	44	0.7640 (0.0076)	0.7615 (0.0076)	-0.188
Tufted Titmouse	14	1.0000 (0.0000)	0.9717 (0.0155)	1.760 *
Eastern Nighthawk	4	0.8944 (0.0444)	1.0000 (0.0000)	-1.422 *

* $0.05 < P < 0.10$

APPENDIX C

LITERATURE REVIEW OF DATA ON MINING SUCCESS OF CAVITY NESTING HOLE-SPACING THAT OCCUR IN THE STUDY AREA

Appendix C Percent estimates of nesting success for study nesting bird species commonly found in the study area

Species	State	Nesting	Mean No. hatched eggs per nest	% hatched eggs per nest	% hatched eggs per nest	Source
Decorative						
Red-tailed Woodpecker	FL	longleaf pine	44	77	—	Stens (1989)
	FL	longleaf pine	140	—	79	J. Kopper, pers. comm.
	IL	mixed deciduous	14	26	—	Reidel (1981)
	MS	redland/pine	34	81	—	Ingold (1981) and cited in Johnson and Korman (1988)
Downy Woodpecker						
	AZ	high elevation conifer	3	100	—	L. and Martin (1981)
	FL	longleaf pine	9	88	—	Stens (1989)
Carolina Chickadee						
	IL	mixed deciduous	21	78	46	Johnson (1982)
	TX	pine/hardwood woodlands	20	70	—	Peter (1988)
Brown-headed Nuthatch						
	FL	cloud pine/scrub	40	60	49.50 ^a	Stens (1987)
Red-crested Flycatcher						
	FL	scrub/deciduous	20	47.50 ^b	—	Taylor and Martin (1981)
Yellow-Throated Vireo						
	AZ	—	21	77	—	Proctor cited in Johnson and Korman (1988)

Species	Sex	Age	Max bone length	% bone length	% body weight	% protein	Source
Larus Blackleg	FL	Adult primary phase	43	10	0.03 ^a	1.06	Blair (1977)
	FL	Adult secondary phase	X	201	0.03 ^a	—	Worm and Woodhouse (1977)
	FL	—	170	41	0.04 ^b	—	Blair (1977) and Woodhouse (1977)
	GA	Adult primary phase	X	29	0.03 ^a	—	Blair (1977)
ME	—	—	27	26	—	—	Prater (1977)
	GA	Adult primary phase	X ^c	200	0.03 ^b	—	Blair (1977)

^a No information.^b Values calculated on a per egg basis instead of per nesting attempt.^c Range given for different phase values.^d Values calculated on a per egg basis instead of per nesting attempt.^e Most nest boxes had several predators present in addition to owls.

BIOGRAPHICAL SKETCH

Karl H. Miller was born and raised in Baltimore, Maryland. He attended Guilford College in North Carolina, where he received a B. A. in art, with a concentration in biology, in 1964. Karl then worked for 4 years as a seasonal employee for the National Park Service and US Forest Service in a variety of environmental interpretation and natural resource management positions. After studying at the School for Field Studies research station in north Queensland, Australia, in 1968, he decided to pursue graduate education. Karl was admitted to the University of Florida in 1969 and graduated with a Master of Science degree in wildlife ecology in December 1971.

Karl graduated from the University of Florida with his doctorate in December 2000. He has conducted research or monitoring projects on woodpeckers, cavity nesting songbirds, American kestrels, Barn Swallows, and house wrens. Although primarily an avian ecologist, Karl also has conducted research on white-tailed deer and Florida manatees.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



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